The theoretical limits to the power output of a muscle–tendon complex with inertial and gravitational loads

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When a muscle delivers power to an inertial load through a spring, the peak power can exceed the maximum that the muscle alone could produce. Using normalized differential equations relating dimensionless quantities we show, by solving the equations either analytically or numerically, that one dimensionless constant ($\mathcal{E}$), representing the inertial load, is sufficient to specify the behaviour during shortening of a muscle–tendon complex with linear force–velocity and force–extension properties. In the presence of gravity, an additional constant (Γ), representing the gravitational acceleration, is required. Nonlinear force–velocity and force–extension relationships each introduce an additional constant, representing their curvature. In the absence of gravity the power output delivered to an inertial load is limited to approximately 1.4 times the maximum power of the muscle alone, and when gravity is present the power delivered is limited to approximately twice the power of muscle alone. These limits are found for the purely inertial load at $\mathcal{E} \approx 1$ and with gravity acting at $\mathcal{E}\Gamma = 0.5$ with $\mathcal{E}$ arbitrarily small. The effects of nonlinear muscle and tendon properties tend to cancel each other out and do not produce large deviations from these optima. A lever system of constant ratio between muscle and load does not alter these limits. Cams and catches are required to exceed these limits and attain the high power outputs sometimes observed during explosive animal movement.

Keywords: muscle; inertial load; power output; tendon

1. INTRODUCTION

The power output of skeletal muscle has a clear limit, but animal movements are sometimes found to use a power beyond this limit (Bennett-Clark 1975; Peplowski & Marsh 1997; Aerts 1998). This could be because extra power is delivered by the recoil of elastic structures in series with the muscle. As pointed out for example by Marsh (1999) the presence of an inertial load is a mechanism that can allow a movement during which the power output of a muscle–tendon complex (MTC) temporarily exceeds that of the muscle alone. Although some examples like this have been modelled (Wilkie 1950; Caldwell 1995; Marsh 1999), there has, to our knowledge, been no previous systematic description of the possible interactions of a muscle, a series compliance and an inertial load. We show in this paper that there are clear limits to the amount of extra power that can be added by tendon recoil in such a system.

2. THE MODEL

The analysis will consider three elements that are mechanically in series: a muscle, an elastic element (a spring) and an inertial load. The movements of the components are summed and the force experienced by each is identical. This force determines the speed of muscle shortening, the length of the spring and the acceleration of the load.

When the functions describing how these quantities depend on the common force have been stated, the system is fully defined, and the movements of the components can be described by appropriate solutions of the differential equations. We will also consider the case where an additional constant force acts on the load only, representing gravity. The initial condition considered is always that the load is at rest. When gravity is absent the initial common force is zero and in the presence of gravity it is equal to the weight of the load. Time zero will represent the start of the muscle activation that produces shortening and movement of the load. We consider first examples that can be solved analytically and then some more complicated cases for which a numerical solution is required.

(a) Dimensional analysis

The use of dimensionless terms to specify a physical system often leads to a simpler solution involving one or more dimensionless constants. Well-known examples are the Froude number and the Reynolds number. Buckingham's theorem (McMahon & Bonner 1983) states that the number of dimensionless constants required is equal to the number of parameters needed to describe the system minus the number of fundamental quantities (mass, length, time, etc.) involved. We will seek to describe each of the systems we discuss using this minimum number of dimensionless constants.

In the linear case to be described, muscle velocity declines linearly with force:

$$V_m = -V_{\max} \left(1 - \frac{F}{F_{\max}} \right); \quad (2.1)$$

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Table 1. Choice of normalizing factors and definition of normalized quantities.

	factor	quantity	dimensionless
force	$F_{\max}$	F	$\varphi = \frac{F}{F_{\max}}$
velocity	$V_{\max}$	V	$\nu = \frac{V}{V_{\max}}$
stiffness	k	k	$1 = \frac{k}{k}$
length	$\frac{F_{\max}}{k}$	L	$\chi = L \frac{k}{F_{\max}}$
acceleration	$\frac{kV_{\max}^2}{F_{\max}}$	$\frac{d}{dt}(V)$	$\frac{d}{d\tau}(\nu) = \frac{d}{dt}(V) \frac{F_{\max}}{kV_{\max}^2}$
time	$\frac{F_{\max}}{kV_{\max}}$	t	$\tau = t \frac{kV_{\max}}{F_{\max}}$
mass	$\frac{1}{k} \left(\frac{F_{\max}}{V_{\max}} \right)^2$	M	$\mathcal{E} = M \left(\frac{V_{\max}}{F_{\max}} \right)^2 k$

length change of the spring is proportional to force:

$$\Delta L_s = F/k, \quad (2.2)$$

and acceleration of the load is proportional to force:

$$\frac{d}{dt}(V_l) = \frac{F}{M}. \quad (2.3)$$

Length is conserved:

$$\Delta L_m + \Delta L_s + \Delta L_l = 0. \quad (2.4)$$

The sign convention is that an increase in the length of the muscle or spring is considered positive and movement of the load towards the spring and muscle is also positive. This system is defined by four parameters, $V_{\max}$, $F_{\max}$, k and M , which represent, respectively, the maximum shortening velocity, the maximum isometric force, the spring stiffness and the mass, and involves the three fundamental quantities mass, length and time. A dimensionless statement of the system should thus be possible using a single parameter. There is no unique method of normalizing the quantities to reach dimensionless expressions. The method we have used is shown in table 1. Because there are three fundamental quantities involved, only three independent choices can be made, represented here by the first three lines in table 1. The other normalizing factors are derived from these three factors by appropriate substitutions.

Equations (2.1)–(2.4) can now be written in dimensionless form as follows:

$$\text{muscle: } \nu_m = \varphi - 1; \quad (2.5)$$

$$\text{spring: } \Delta \chi_s = \varphi; \quad (2.6)$$

$$\text{load: } \frac{d}{d\tau}(\nu_l) = \frac{\varphi}{\mathcal{E}}; \quad (2.7)$$

$$\text{length conservation: } \Delta \chi_m + \Delta \chi_s + \Delta \chi_l = 0. \quad (2.8)$$

The four parameters have been reduced to one, $\mathcal{E}$, representing the ‘dimensionless mass’ in the system. A sol-

ution of these equations will therefore provide a description for all possible combinations of $V_{\max}$, $F_{\max}$, k and M .

3. RESULTS

(a) *First case: linear motion; spring and muscle characteristics linear*

The ordinary differential equation describing this system can be obtained by substituting into the time derivative of equation (2.8) the corresponding derivatives of equations (2.5)–(2.7). This gives

$$\frac{d^2}{d\tau^2}(\nu_l) + \frac{d}{d\tau}(\nu_l) + \frac{1}{\mathcal{E}}(\nu_l) - \frac{1}{\mathcal{E}} = 0.$$

The solution of this equation is

$$\nu_l = 1 - \frac{e^{-\frac{\tau}{2}}}{2Q} (2Q \cos(Q\tau) + \sin(Q\tau)),$$

where $Q = \sqrt{1/\mathcal{E} - 1/4}$. The value of Q is real when the mass $\mathcal{E}$ is less than 4 and imaginary when $\mathcal{E}$ is greater than 4. When $\mathcal{E} = 4$ the velocity is given by

$$\nu_l = 1 - e^{-\frac{\tau}{2}} \left(1 + \frac{\tau}{2} \right).$$

The force can be found by differentiating these equations and multiplying by $\mathcal{E}$ to give

$$\begin{aligned} \varphi &= e^{-\frac{\tau}{2}} & \text{if } \mathcal{E} = 4, \\ &= \frac{1}{Q} e^{-\frac{\tau}{2}} \sin(Q\tau) & \text{otherwise.} \end{aligned}$$

Q represents the ‘angular velocity’ of the system and when $\mathcal{E}$ is less than 4 the force will return to zero when $t = \pi/Q$. The ways in which force and velocity depend on $\mathcal{E}$ are illustrated in figure 1. Two special cases are of interest: when $\mathcal{E} = 4$ (dashed line) the system is ‘critically damped’; this is the lowest value of $\mathcal{E}$ for which the velocity does not exceed unity. In the case that $\mathcal{E}$ tends to

Figure 1. Time-courses of (a) load velocity, (b) force and (c) power delivered to the load for seven values of the normalized inertial load (Ξ). From left to right the lines are for Ξ values of 1/64, 1/16, 1/4, 1 (solid line), 4 (dashed line), 16 and 64.

infinity (not shown in the figure) the force exponentially approaches unity with unit rate constant, and the velocity remains infinitesimal.

When Ξ is less than 4 the peak load velocity exceeds $V_{\max}$. Peak load velocity occurs when the force drops to zero, and at that instant $v_l = 1 + e^{-\pi/2Q}$. For infinitely small normalized inertial loads, Q becomes infinitely large and peak v_l becomes two, i.e. the infinitesimal inertial load can be accelerated up to a maximum speed of twice the muscle's maximal shortening velocity.

The power delivered to the load is the product of force and load velocity. Some representative power-output curves are shown in figure 1c. The maximum power that the muscle alone can produce is 0.25 normalized units, which is the product of force and velocity at the midpoint of their relationship (equation (2.5)). Figure 2 shows, as a function of Ξ , the peak power generated as a ratio to this value. The maximum value of this 'power amplification' by the inertia-spring system is 1.436 (to three decimal places) and occurs at a value of Ξ very close to one.

Figure 2. Ratio of the peak power output of the MTC to the value for the muscle alone. Solid line, without gravity; dotted curves, with gravity at $\Gamma = 10$ (left) and $\Gamma = 1$ (right).

The full lines in figure 1 show the time-courses of the mechanical events during a contraction that produces the greatest possible power amplification. Early in the contraction the muscle moves faster than the load and, as a result, while force is rising, the muscle power is mostly used to increase the elastic energy in the spring. After the peak force the load is moving faster than the muscle and the spring recoil adds energy from the spring to the continuing power output of the muscle, thus providing the optimum power delivery to the load. Peak power thus occurs while force is falling and at this point the muscle has shortened by 1.089 units.

(b) *Second case: rotary motion inertial load; spring and muscle characteristics linear*

The equations given in §§ 2 and 3a will apply if F represents the torque, V the angular velocity, L the angular movement and M the moment of inertia of the load. The system for normalization works as above with Ξ giving the normalized moment of inertia.

An interesting case is when the muscle and spring are connected to the load via a lever so that the force in the muscle and spring is R times the force on the load. In this case the same equations will apply except that Ξ is given by $M(V_{\max}/F_{\max})^2 k R^2$. It follows that in these cases the maximum power amplification is also 1.436.

(c) *Third case: linear motion; inertial and gravitational loading; linear muscle and spring*

In this case the load experiences an additional acceleration caused by gravity and equation (2.7) becomes

$$\frac{d}{d\tau}(v_l) = \frac{\varphi}{\Xi} - \Gamma,$$

where Γ is the normalized acceleration due to gravity, which is the usual gravitational acceleration g divided by the appropriate normalizing factor. The subscript Γ indicates the presence of a gravitational force.

The ordinary differential equation describing this system is

Figure 3. Peak power output as a function of the normalized weight of an inertial and gravitational load. Solid line, $\Gamma = 1$; dashed line, $\Gamma = 10$; dotted line, $\Gamma = 100$. The two lower values of Γ are as in figure 2.

$$\frac{d^2}{d\tau^2}(v_{lr}) + \frac{d}{d\tau}(v_{lr}) + \frac{1}{\Xi}v_{lr} + \Gamma - \frac{1}{\Xi} = 0.$$

The solution of this equation (from the time at which the force in the muscle equals the weight of the load) is

$$v_{lr} = (1 - 4\Gamma) \left(1 - e^{-\frac{\tau}{2}} \left(1 + \frac{\tau}{2} \right) \right) \quad \text{if } \Xi = 4,$$

$$= (1 - \Xi\Gamma) \left[1 - \frac{e^{-\frac{\tau}{2}}}{2Q} (2Q \cos(Q\tau) + \sin(Q\tau)) \right] \quad \text{otherwise.}$$

The force in the spring is found by differentiating the velocity and multiplying by Ξ to obtain

$$\varphi_r = (1 - 4\Gamma) \tau e^{-\frac{\tau}{2}} + 4\Gamma \quad \text{if } \Xi = 4,$$

$$= (1 - \Xi\Gamma) \frac{e^{-\frac{\tau}{2}}}{Q} \sin(Q\tau) + \Xi\Gamma \quad \text{otherwise.}$$

Notice that the above expressions for the load velocity and force in the spring can be expressed as functions of the velocity and force, respectively, in the absence of gravity (see § 3a):

$$v_{lr} = (1 - \Xi\Gamma) v_l$$

and

$$\varphi_r = (1 - \Xi\Gamma) \varphi + \Xi\Gamma.$$

Figure 2 shows peak power as a function of normalized inertial load for three values of Γ . The peak power is higher in the presence of gravity and occurs at lower values of Ξ . Figure 3 shows the peak power as a function of the normalized weight (that is, $\Xi\Gamma$). Peak power for high values of Γ occurs when the weight is 0.5. The limiting value of the peak power is 2.0 and occurs when Γ is very large.

In the presence of gravity, higher peak power amplifications can be achieved with less energy released from the spring than when gravity is absent (figure 4). Increasing the gravitational acceleration reduces the work that is

Figure 4. Peak power ratio as a function of the work done by the spring. Solid curve, purely inertial load; broken curve, optima for different gravitational loads. Higher optimal values correspond to higher gravitational loads. Dots, optima from the three curves in figure 3.

delivered from the spring to the load under conditions for optimum power.

(d) *Fourth case: linear motion inertial load; spring and muscle nonlinear*

We have not found useful analytical equations for describing the behaviour of these systems when the muscle force-velocity and/or the spring force-extension relations are nonlinear, as they are in real animals. We have therefore used numerical methods to solve the appropriate differential equations for some interesting cases.

Equation (2.1) can be replaced by the force-velocity relation expressed by Hill's equation:

$$V_m = V_{\max} \frac{1 - (F/F_{\max})}{1 + G(F/F_{\max})}.$$

When $G = 0$, the relation reduces to equation (2.1) and the force-velocity relation is linear; as G increases the force-velocity relation becomes more curved. The maximum power that the muscle can produce falls as G rises.

Using the other differential equations as given above (equations (2.2) and (2.3)) we have calculated the force and velocity of the load for a range of loads using a fourth order Runge-Kutta method implemented in MATHCAD. The accuracy of the solutions was checked against the analytical solution for the linear case. G values from 0 to 10^6 were investigated. The peak power expressed relative to the maximum muscle power increases as G increases. For very high values of G a limiting value is reached, which is approximately 1.473, *ca.* 3% greater than the value of 1.436 for the linear force-velocity relation. The case shown in figure 5 is for $G = 4$, which is similar to the values found in actual muscle (Woledge *et al.* 1985).

The force-extension relation of the spring is also likely to be nonlinear in real animals, where the spring consists largely of tendon. To investigate the influence of this

Figure 5. The relationship between the logarithm of the normalized inertial load and the peak power ratio. Solid curve, muscle and spring linear; triangles, nonlinear muscle force-velocity relationship ($G = 4$); circles, nonlinear spring force-extension relationship ($H = 4$).

factor we have replaced equation (2.2) with the hyperbolic function:

$$F = \frac{kL_s}{1 + H[1 - (kL_s/F_{\max})]}.$$

When $H = 0$ the function is linear and with $H = 4$ the function is a reasonable approximation to the actual shape of tendon stress-strain curves. The maximum power output (with linear force-velocity relation) is changed by this non-linearity of the force-extension curve of the spring. The maximum power is reduced by *ca.* 10% in this example. We have investigated a range of H values up to 32. All these values give peak powers of less than the optimum with a linear force-extension curve.

In actual animals both the force-velocity and the force-extension relationships will be curved. The opposite changes in maximum power output relative to the muscle power delivered to an inertial load will tend to cancel and the resulting power output could be expected to be within a few per cent of the values for the linear case.

(e) Fifth case: catches

If the movement of the load is restricted by a catch, the force in the spring can increase to the maximum force the muscle can develop. If the catch is now released, the force in the spring will accelerate the load and the energy in the spring will be converted to kinetic energy of the load. Although the muscle can add some power during the recoil process, the speed of shortening of the muscle is not limiting and the rate at which this energy will be transferred from spring to load is determined primarily by the mass and the spring stiffness as described by the familiar equation of simple harmonic motion: $\sin(t\sqrt{K/M})$, or in our dimensionless form: $\sin(\tau/\sqrt{\Xi})$.

The peak power therefore rises without limit as the value of Ξ approaches zero (figure 6). The dashed curve shows how the peak power of a system containing a catch changes with the value of Ξ . For all values of Ξ up to at

Figure 6. The relationship between the logarithm of the normalized inertial load and the peak power ratio. Solid curve, without catch; dashed line, with a catch released from $F_{\max}$.

least 3 ($\sim 10^{0.5} \Xi$ units) a catch mechanism can deliver a higher peak power than the inertial mechanism alone.

A cam is a mechanism by which the lever ratio (R in § 3b) varies as the rotation proceeds. If R is made to decrease, the action of the mechanism is analogous to that of a catch: at early times the force in the muscle and spring is large compared with that acting on the load, with the full force of the tendon applied to the load only later in the process. The power outputs of cam mechanisms will then fall between those of the inertial mechanisms and those of the catch mechanism shown in figure 6.

4. DISCUSSION

Muscle and tendon behaviours have been described here using only force-velocity and force-extension relationships, respectively. Not included are the force-length relationship, activation-relaxation time-course, contractile depression resulting from shortening, and tendon force-extension hysteresis, all of which may limit power output in animals. Muscle shortening and load movement have not been constrained by any mechanical arrangement, as may be the case during animal movement. The simplicity of our model reveals the fundamental principles underlying the mechanical interactions between muscle, tendon and loads, but it remains to be discussed whether actual muscles, subject to the above additional constraints, could make use of the mechanism for power amplification. How far does a muscle have to shorten to achieve the maximum velocity of the load with a contraction giving the greatest possible power output? Is this shortening within the range permitted by the force-length relationship? Is the time of muscle action sufficient to allow for its full activation? These questions are best addressed by considering a dimensioned example.

The human triceps surae muscle group can generate a maximal static moment of *ca.* 200 Nm around the ankle and shorten at a maximal velocity of *ca.* 8 rad s⁻¹ (Bobbett & Van Ingen Schenau 1990). These values are

equivalent to 4000 N and 0.4 m s^{-1} in line with the muscle, using an Achilles tendon moment arm of *ca.* 0.05 m (Fukunaga *et al.* 1996). An estimate of the Achilles tendon stiffness ($120\,000 \text{ Nm}^{-1}$) can be obtained from fig. 6 in Kurokawa *et al.* (2001). Using these parameter values the optimal mass for power amplification ($\mathcal{E} = 1$) is *ca.* 800 kg applied directly at the muscle. The optimal mass at the foot assuming a lever ratio of four from the Achilles tendon is *ca.* 50 kg, i.e. not far from the average body mass. The fascicle shortening required to achieve maximal power is *ca.* 0.04 m. The resting fibre length in the human triceps surae muscle seems to range from 0.035 to 0.075 m (Maganaris *et al.* 1998). It would therefore be possible for the triceps surae, when opposed by an inertial load, to be used in a way in which power amplification would be effective, and not far from the optimum, although perhaps peak power delivery may be constrained by the dimensions of the fibres. For optimum loading the peak power would be reached two normalized time units after muscle activation, which in this example corresponds to *ca.* 170 ms, which is a similar interval to that reported for the human push off using the triceps surae muscles (Kawakami *et al.* 2002).

It has been shown that the most important determinant of the dimensionless behaviour of an MTC acting against an inertial load, and, as a result, of the maximum power that can be delivered to that load, is the dimensionless inertial load, $\mathcal{E}$. Its value depends not only on the magnitude of the inertia, but also on the muscle and spring properties in the way shown in table 1 for linear-motion load. For rotational-motion load the lever ratio is also involved in the way shown in § 3b. This result has implications for normalizing loads used during experiments. It is common to express the gravitational load relative to the muscle's maximum isometric force. However, expressing the load in dimensionless terms must also include normalization of its inertial component relative to the muscle, spring and lever characteristics of the system.

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