

SHORT COMMUNICATION

POWER OUTPUT FROM SKELETAL MUSCLE DURING LINEAR AND SINUSOIDAL SHORTENING

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Several recent accounts have estimated the maximum sustainable mechanical power available from a skeletal muscle based on measured or assumed force–velocity characteristics of the muscle and the assumption that the muscle, when active, shortens constantly at the velocity that is optimal for power output. Curtin and Woledge (1988) used this approach in estimating how much mechanical power is available from the myotomal muscles of a dogfish to power swimming. The muscles of a fish operate cyclically, shortening and doing work for half a cycle and being lengthened, possibly absorbing work, for the other half-cycle. Curtin and Woledge allowed for the periodic nature of power output by assuming that only half the muscles were active at any time, which is equivalent to assuming that the sustainable power is half the peak power. During swimming, the shape of the trunk of a fish changes sinusoidally with time (Hess and Videler, 1984), and the shortening velocity of a trunk muscle fiber must also vary approximately sinusoidally. Thus shortening velocity cannot be at the optimum velocity for power output through the entire shortening half-cycle: the assumption of shortening at a constant, optimum velocity must overestimate the power output. Weis-Fogh and Alexander (1977) and Pennycuik and Rezende (1984) have also estimated the maximum sustainable power output of muscle based on the assumption of shortening at constant velocity. The principal muscles considered in the latter two studies were flight muscles. For flight muscles, as for swimming muscles, a sinusoidal length trajectory and a sinusoidally varying shortening velocity are more realistic assumptions than a linear length change and a constant velocity of shortening. The following analysis was begun to determine the magnitude of the error that is likely to enter into estimates of power output from the assumption that muscle shortening during normal locomotion is at constant velocity rather than at a velocity which varies sinusoidally with time. It is shown that the assumption of shortening at constant velocity overestimates maximum power output by 20% or less.

In determining the maximum power output available during linear shortening

Key words: muscle, work, power, strain.

and during sinusoidal shortening, it is assumed that the force-velocity relationship for the muscle is described by the Hill hyperbola:

$$(F + a)(V + b) = (F_0 + a)b, \quad (1)$$

where F is muscle force, V is shortening velocity, F_0 is the maximum isometric muscle force and a and b are constants. It is assumed that the shortening and lengthening half-cycles of the muscles are of equal duration, that the muscle becomes fully active instantaneously at the beginning of the shortening half-cycle, and that it relaxes instantaneously at the beginning of the lengthening half-cycle so that the muscle offers no resistance to lengthening. It is assumed further that the force-velocity characteristics of the muscle do not change with muscle length. This assumption would be true if the muscle operated entirely on the plateau of a length-tension curve. The assumption of constant force-velocity characteristics will overestimate the maximum power output for both sinusoidal and linear shortening at low frequencies, where the strain per cycle at optimum conditions is large and the length range will include significant portions of the ascending and descending limbs of the length-tension curve. The expected force and velocity trajectories for a muscle during sinusoidal and during linear shortening are illustrated in Fig. 1.

Linear shortening. Solving the Hill equation (1) for velocity (V), and multiplying the result by force (F) to obtain the power output, P , gives:

$$P = FV = Fb \left[\frac{F_0 - F}{F + a} \right]. \quad (2)$$

Differentiating equation 2 with respect to F , setting the result equal to 0 and solving for F gives the optimum force, F^* for power output:

$$F^* = \sqrt{a^2 + F_0 a} - a. \quad (3)$$

For many muscles the product aF_0^{-1} is 0.2-0.4 and F^* is about one-third of F_0 . Replacing F with F^* in equation 2 gives P_{\max} , the peak instantaneous power

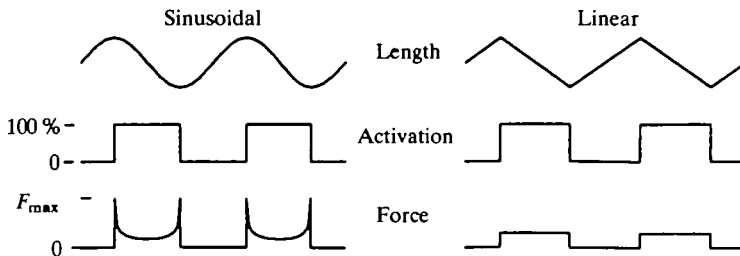


Fig. 1. Expected muscle force during sinusoidal shortening (left) and during shortening at constant velocity (right). In both cases it is assumed that the muscle is fully active during the shortening half-cycle, and fully inactive and totally compliant during muscle lengthening. The values used in constructing these curves were: frequency 5 Hz; aF_0^{-1} , 0.2; V_{\max} , 5 L s^{-1} , where L is muscle length. The total strain for the sinusoidal trajectory (14%) is the optimum for work output, as is the shortening velocity (1.45 L s^{-1}) in the linear model.

available from the muscle. For the cyclically contracting muscle, the maximal sustainable power output is $0.5P_{\max}$ and is independent of operating frequency. It is half the peak value because the muscle shortens for half the cycle and is lengthened over the other half; it is independent of frequency because over any time interval containing an integral number of cycles the muscle shortens for half the time and lengthens for the other half, no matter what the frequency.

Sinusoidal shortening. The following relationship for the work output per cycle during sinusoidal shortening (W_s) is based on Josephson and Stokes (1989):

$$W_s = \int_{-\Delta S}^{+\Delta S} \left[\frac{(F_0 + a)b}{\Delta S_0 \omega \sqrt{1 - (\Delta S / \Delta S_0)^2 + b}} - a \right] d(\Delta S), \quad (4)$$

where ΔS is muscle strain, measured from the average muscle length. If L is the absolute muscle length and L the average muscle length (the muscle length at the mid-point of the sinusoidal length change), $\Delta S = (L - L) / L$. ΔS_0 is the maximum value of ΔS and ω is the angular velocity ($= 2\pi \times$ frequency). The other symbols are as defined above.

The total power output is the work done per cycle, W_s , times the operating frequency. It should be noted that W_s is inversely related to operating frequency, and that it is a function of the strain per cycle (total strain per cycle $= 2\Delta S_0$). It has been shown that there is an optimum strain per cycle for work output (Josephson and Stokes, 1989).

The work output at a given frequency was evaluated for a set of strain values using equation 4 to determine empirically the optimum strain and the maximum work output and the maximum power output at that frequency. The work output was calculated with MathCAD (MathSoft, Inc., Cambridge, MA), a computer program which allows evaluation of integrals. Optimum strain and maximum power output were determined for a set of values of operating frequency, of a (expressed as aF_0^{-1}) and of maximum shortening velocity ($V_{\max} = bF_0 a^{-1}$). V_{\max}

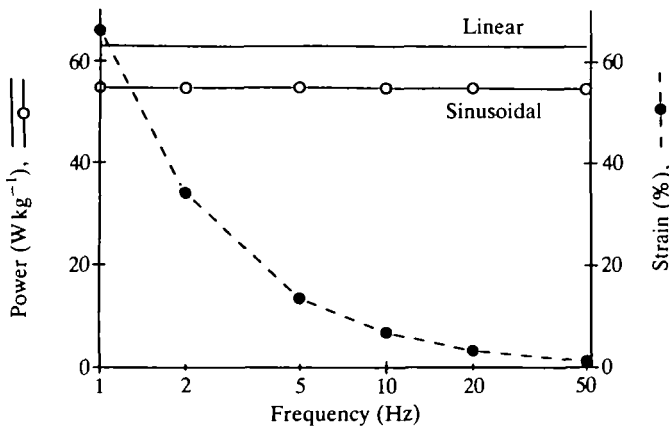


Fig. 2. Maximum power output during linear and sinusoidal shortening, and the optimum strain for power output during sinusoidal shortening. The muscle parameters were: F_0 , 30 N cm^{-2} ; aF_0^{-1} , 0.2 ; V_{\max} , 5 L s^{-1} , where L is muscle length.

Table 1. Power output during sinusoidal shortening relative to that during linear shortening, and the optimum strain during sinusoidal shortening

V_{\max} ($L s^{-1}$)	a/F_0	Linear power ($W kg^{-1}$)	Sinusoidal power/linear power (Optimum strain)					
			1 Hz	2 Hz	5 Hz	10 Hz	20 Hz	50 Hz
1	0.05	4.8	0.90 (9%)	0.90 (4.8%)	0.91 (1.6%)	0.91 (1.0%)	0.92 (0.5%)	0.96 (0.24%)
1	0.2	12.6	0.87 (13%)	0.87 (7%)	0.87 (2.6%)	0.87 (1.2%)	0.87 (0.7%)	0.88 (0.28%)
1	1	25.7	0.83 (18%)	0.83 (8.8%)	0.83 (3.6%)	0.83 (1.6%)	0.84 (0.9%)	0.84 (0.36%)
5	0.05	24.1	0.90 (45%)	0.90 (22%)	0.90 (8.8%)	0.91 (4.4%)	0.91 (2.3%)	0.91 (0.9%)
5	0.2	63.0	0.87 (65%)	0.87 (34%)	0.87 (14%)	0.87 (7.0%)	0.87 (3.5%)	0.87 (1.2%)
5	1	128.7	0.83 (88%)	0.83 (42%)	0.83 (18%)	0.83 (8%)	0.83 (4.5%)	0.83 (1.8%)
20	0.05	96.3	0.90 (180%)	0.90 (90%)	0.90 (36%)	0.90 (18%)	0.90 (9%)	0.91 (3.6%)
20	0.2	252.1	— —	0.87 (132%)	0.87 (53%)	0.87 (27%)	0.87 (13%)	0.87 (5.2%)
20	1	514.7	— —	0.83 (176%)	0.83 (70%)	0.83 (35%)	0.83 (18%)	0.83 (7%)

The maximum muscle stress, F_0 , was $30 N cm^{-2}$.

Two sets of entries at high shortening velocity and low frequency are missing because the optimum strain exceeded twice the muscle length, which would require the shortest length reached by the muscle to be less than 0.

L is muscle length.

was chosen as a measure of velocity characteristics rather than b because it is a more familiar parameter. The range of parameters examined encompasses the values likely to be encountered in animal muscles and locomotion: frequency 1, 2, 5, 10, 20, 50 Hz; aF_0^{-1} 0.05, 0.2, 1; V_{\max} 1, 5, 20 muscle lengths per second ($L s^{-1}$).

The work per cycle with sinusoidal shortening declined with frequency, but the maximum power output was nearly independent of frequency (Fig. 2, Table 1). For linear shortening at a constant velocity the strain per cycle is necessarily inversely proportional to cycle frequency. With sinusoidal shortening the optimal strain for work output was approximately inversely proportional to frequency. As expected, the maximum power output during sinusoidal shortening was less than that which would be obtained with linear shortening at the optimum velocity, but the difference in power output between linear and sinusoidal length trajectories

was not great. Through almost the entire range of parameters examined the maximum power output during sinusoidal shortening was 83–92 % of that during linear shortening. Given the usual uncertainties about values determined in force–velocity measurements, a 10–20 % error due to an imperfect model is not very large. Half the peak instantaneous power from a force–velocity curve is a reasonable estimate of the maximum sustainable power during sinusoidal shortening.

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