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Review

The efficiency of muscle contraction

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Abstract

When a muscle contracts and shortens against a load, it performs work. The performance of work is fuelled by the expenditure of metabolic energy, more properly quantified as enthalpy (i.e., heat plus work). The ratio of work performed to enthalpy produced provides one measure of efficiency. However, if the primary interest is in the efficiency of the actomyosin cross-bridges, then the metabolic overheads associated with basal metabolism and excitation–contraction coupling, together with those of subsequent metabolic recovery process, must be subtracted from the total heat and work observed. By comparing the cross-bridge work component of the remainder to the Gibbs free energy of hydrolysis of ATP, a measure of thermodynamic efficiency is achieved. We describe and quantify this partitioning process, providing estimates of the efficiencies of selected steps, while discussing the errors that can arise in the process of quantification. The dependence of efficiency on animal species, fibre-type, temperature, and contractile velocity is considered. The effect of contractile velocity on energetics is further examined using a two-state, Huxley-style, mathematical model of cross-bridge cycling that incorporates filament compliance. Simulations suggest only a modest effect of filament compliance on peak efficiency, but progressively larger gains (vis-à-vis the rigid filament case) as contractile velocity approaches V_{max}. This effect is attributed primarily to a reduction in the component of energy loss arising from detachment of cross-bridge heads at non-zero strain.

Keywords: Energy; Enthalpy; Efficiency; Cross-bridges; Fibre-type; Species-differences

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Nomenclature

α	forward rate constant
ADP	adenosine diphosphate
AMP	adenosine monophosphate
ATP	adenosine triphosphate
β	reverse rate constant
b	limit of cross-bridge negative strain (at which elastic energy exceeds ΔG_{ATP})
Cr	creatine
ΔE	change of energy
ΔG	change of Gibbs free energy
$\Delta G^{\mathrm{o}}_{\mathrm{ATP}}$	change of standard Gibbs free energy of ATP hydrolysis
ΔG_{ATP}	change of Gibbs free energy of ATP hydrolysis
$\Delta l, \Delta L$	change of muscle length
ΔH	change of enthalpy (work + heat)
$\Delta H_{\mathrm{ATP}}, \Delta H_{\mathrm{PCr}}$	enthalpy of ATP, PCr hydrolysis
ΔS	change of entropy
EDL	*extensor digitorum* muscle
ε	efficiency (work/enthalpy)
ε_{I}	efficiency of initial metabolism
$\varepsilon_{\mathrm{Net}}$	efficiency of initial plus recovery metabolism
ε_{R}	efficiency of recovery metabolism
$\varepsilon_{\mathrm{Overall}}$	efficiency of basal plus initial plus recovery metabolism
η	thermodynamic efficiency ($W/\Delta G$)
η_{X-b}	thermodynamic efficiency of cross-bridge cycling
F	force (see, also, P and T)
f	x-dependent rate of attachment of cross-bridges in Huxley's (1957) model
g, g_1, g_2	x-dependent rates of detachment of cross-bridges in Huxley's (1957) model
h	maximal extent of cross-bridge displacement from $x = 0$
H_{o}	maximal rate of isometric enthalpy production
J	cross-bridge flux
k	cross-bridge stiffness; Boltzmann's constant
K	equilibrium constant (of the creatine phosphotransferase reaction)
p_{A}	proportion of initial heat attributable to activation of contraction
p_{R}	proportion of metabolic heat attributable to recovery processes
p_{stim}	proportion of suprabasal heat attributable to the stimulus
P	force or stress or tension (see, also, F and T)
$P_{\mathrm{o}}, T_{\mathrm{o}}$	maximal isometric force
PCr	phosphocreatine
Pi	inorganic phosphate
PV	product of force and velocity, power ($\mathrm{J\,s^{-1}}$)
Q	heat (J)
$Q_{\mathrm{A}}, Q_{\mathrm{I}}, Q_{\mathrm{R}}$	activation, initial, recovery heat