THE INFLUENCE OF TENDON COMPLIANCE ON MUSCLE POWER OUTPUT AND EFFICIENCY

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INTRODUCTION

When large animals run or walk, they often do so with an efficiency greater than can be accounted for by the efficiencies of the muscles powering the movement. One factor that may account for this observation is the contribution of elastic tendons to power output. We tested the hypothesis that a tendon of appropriate compliance connected in series with a muscle can increase the power output while maximising muscle efficiency.

METHODS

Experiments were performed using isolated muscle fibre bundles connected in series with artificial tendons (made of latex strips) of varying compliance. Muscle length was varied in a sinusoidal pattern at physiological frequencies with brief periods of stimulation (of varied duration and phase with respect to the length changes) in each length change cycle. Work and power outputs were calculated from measurements of force output and change in muscle-tendon length. The heat produced by the muscles was measured using a thermopile. The sum of the work and heat produced (i.e. the enthalpy output) is proportional to the amount of ATP used. Initial mechanical efficiency (excluded recovery metabolism) was calculated as the ratio of the power output to the rate of enthalpy output[1]. We determined the optimum stimulation timing that maximised net muscle power output in each tendon compliance condition and used a MANOVA to determine the influence of the tendon compliance, amplitude of length change and duration of stimulation on the net power, peak power, enthalpy and efficiency.

RESULTS AND DISCUSSION

In each tendon compliance condition, the optimum timing to maximise net power output was found to be 25 ms before shortening occurred (5% of the total cycle time). There was no significant difference between any of the dependent variables and the duration of stimulations tested. Tendon compliance was shown to have a significant effect on the net power output ($P<0.001$), peak power ($P<0.001$), net enthalpy ($P<0.001$) and efficiency ($P<0.001$) when sufficient length changes were used to maximise net power output. In each case, increasing tendon compliance increased both the power and efficiency (Table 1). Amplitude of length change had a significant effect on the dependent variable, with more compliant conditions requiring greater length changes to maximise net power output.

The most compliant tendons increased the peak power output of the muscle by more than four times that which can be achieved by the muscle fibres alone under steady state conditions (~$0.4P_0L_0$/s). This was possible because the tendon underwent the majority of the shortening as it returned stored elastic energy. Net power must be generated by the muscle fibres alone (since elastic energy stored should be the same at the start and the end of the cycle), therefore increasing compliance allowed the muscle to generate more work in each cycle. An analysis which separated the length changes of the muscle fibres from the tendons (by calculating the strain of the tendon) indicated that the mean shortening velocity during positive power production (~1.3 lengths/s) was closer to the optimal velocity for maximising power output and efficiency in the most compliant tendon conditions compared to the least compliant conditions (~0.5 lengths/s). This demonstrates the importance of having compliant tendons so that muscles may act at more favourable speeds to maximise power output and efficiency.

CONCLUSIONS

Increasing tendon compliance increased the power output and efficiency of muscle, providing that the muscle was sufficiently stretched and activated appropriately.

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REFERENCES

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Table 1: Average (±sem) peak power, net power, net enthalpy and efficiency for each compliance condition at lengths where net power is maximised. Tendon compliance (measured in $mm.mN^{-1}$) is represented as dimensionless number by multiplying it by the quotient of maximum isometric force (P_0) and muscle fibre optimum length (L_0). Units of power are normalised to P_0 and L_0.

Dimensionless Tendon Compliance	Peak Power (P_0L_0/s)	Net Power (P_0L_0/s)	Net Enthalpy (P_0L_0/s)	Efficiency (%)
0.285	1.305 (0.094)	0.199 (0.009)	0.579 (0.021)	34.5 (1.3)
0.1	1.820 (0.089)	0.139 (0.013)	0.416 (0.029)	34.9 (1.7)
0.05	0.825 (0.028)	0.111 (0.009)	0.337 (0.027)	31.9 (1.3)
0.0286	0.625 (0.036)	0.086 (0.006)	0.383 (0.022)	25.9 (2.0)