For commonly employed muscle-tendon-complex models, predictions of human metabolic energy expenditure are substantially lower than measured values at the single-joint level

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Musculoskeletal models can be viable tools for addressing hypotheses regarding the role of metabolic energy expenditure in human (loco)motion. The Hill-type muscle-tendon-complex (MTC) model is commonly employed for this purpose, even though in this model a conceptual link between mechanics and energetics is lacking. In contrast, this link is present in Huxley-type MTC models, but it is less well established for this class of models that mechanical behavior is adequately described. The purpose of this study was to evaluate how well a Hill and a Huxley MTC model can predict the mechanical behavior and the metabolic energy expenditure of human leg muscles, using data collected for this purpose on human subjects.

We measured oxygen consumption and the net knee joint moment in 4 physically fit male adult subjects who performed a kinematically constrained single leg knee flexion/extension task. Prior to this, we measured subjects’ maximal moment-knee angle relationship and resting oxygen consumption. The task consisted of 3 minutes flexion/extension between 25 and 95 degrees of knee flexion (0 degrees corresponding to completely stretched leg) and was performed at two isokinetic angular velocities (50 and 70 deg/s). Subjects were instructed to deliver force in the direction of the movement, and to choose the intensity level such that they could maintain this for 3 minutes. In order to minimize net tendon work within each half-cycle, subjects were also instructed to deliver zero force around the minimal and maximal knee angles. With the aid of visual feedback of their moment-time curve, subjects managed to maintain a steady moment-time curve over all cycles within one trial. EMG signals were obtained from the quadriceps (Quad) and hamstrings (Hams) muscles; it was found that co-contraction was negligible during the task. Overall, the experimental conditions were such that the measured external mechanical work was representative of the positive muscle fiber work, and could thus be meaningfully related to metabolic energy expenditure. The imposed task did not induce steady state oxygen consumption. Therefore, the total oxygen consumption (including ‘recovery’ oxygen consumption) was related to the net mechanical work done during the task.

A planar, 1 DOF model consisting of an upper and a lower leg was used to relate the knee angle and moment to the Quad and Hams muscles’ length and force. For both muscles, a Hill and a Huxley type MTC model was constructed according to Umberger et al. (2003) and Lemaire et al. (2016), respectively. For both models, parameter values were obtained partly from the experimental data and partly from the literature. Specifically, for the Huxley MTC model, parameters were chosen such that the steady state force-velocity relationship was the same as that for the Hill MTC model and parameters governing the prediction of metabolic energy expenditure were taken from Lemaire et al. (2016b). Key subject specific parameter values obtained from the isometric moment – knee joint angle relationships are listed in table 1.

Table 1. m. Quadriceps and m. Hamstrings physiological characteristics. Maximal isometric force ($F_{\max}$), optimum Contractile Element length ($l_{\mathrm{CE}}^{\mathrm{opt}}$) and mass, according to Umberger et al. (2003). Values are mean (SD).

	$F_{\max}$ (N)	$l_{\mathrm{CE}}^{\mathrm{opt}}$ (cm)	$Mass$ (kg)
m. Quadriceps	5500 (1300)	8.3 (1.5)	1.9 (0.4)
m. Hamstrings	5000 (500)	7.0 (2.5)	1.5 (0.6)

Simulations were done for both models and task conditions. For each participant and each condition, muscle stimulation as a function of time ($stim(t)$, model input) was chosen such that the difference between the model-predicted and the averaged experimentally recorded moment-time curve was minimized, resulting in an RMS difference < 5 Nm for all subjects and conditions. After normalization by their own respective time integrals, $stim(t)$ closely matched the measured rectified and low-pass filtered EMG signal, for all comparisons. Thus, both models adequately captured the mechanical properties of the muscle. Results regarding predicted and measured mechanical work and metabolic energy expenditure, lumped for both muscles, are reported in Table 2.

Table 2. Summary of main results. Measured (Data) and measured minus modelled (Data – Hill and Data – Huxley) mechanical power output ($\boldsymbol{P}_{\mathbf{mech}}$) and baseline subtracted metabolic power ($\boldsymbol{P}_{\mathbf{met,net}}$), for both conditions. Values are mean (SD) in Watts.

		Data	Data – Hill	Data – Huxley
50 deg/s	P_{mech}	37 (6)	1 (1)	-1 (1)
	$P_{\mathrm{met,net}}$	254 (49)	228 (26)	139 (40)
70 deg/s	P_{mech}	47 (8)	0 (0)	-1 (2)
	$P_{\mathrm{met,net}}$	447 (108)	313 (89)	238 (94)

The primary finding was that for both MTC models, metabolic energy expenditure was substantially underestimated. Furthermore, the error for the Hill MTC model was much larger than that for the Huxley MTC model. Since we subtracted resting oxygen consumption, the measured metabolic energy consumption is an upper limit to the actual energy consumption of the muscles; this may in part explain the observed difference. Another possible explanation of the observed difference is that not all muscle mass was activated during the task; any underestimation of the active muscle mass will lead to an underestimation of metabolic energy expenditure, as the latter scales linearly with the former. However, it is unlikely that any of the above can account for the magnitude of the differences observed here. Another possibility to consider is that the original data with which the models were parameterized is not representative for the type of contractions or organism considered in this study; the models in their current form may simply not be suited for prediction of metabolic energy expenditure during the task considered here. If the latter were to be the case, the results of this study are cause for concern, because similar models are commonly used for modelling metabolic energy expenditure during human locomotion. In our view, it is urgent to determine which aspects of the models are key to the observed difference.

References

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Video url: https://www.youtube.com/watch?v=w_zvZX--PWk&t=13s