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Stance and Swing Phase Costs in Human Walking

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Nomenclature

A_{AM}	activation/maintenance heat rate scaling factor
A_S	shortening heat rate scaling factor
CE	contractile element
$\dot{E}$	rate of muscle metabolic energy expenditure
F_{CE}	contractile element force
F_{ISO}	scaled contractile element force-length curve
$\%FT$	percentage of fast twitch fibers
$\dot{h}_A$	activation heat rate
$\dot{h}_{AM}$	combined activation and maintenance heat rates
$\dot{h}_M$	maintenance heat rate
$\dot{h}_{SL}$	shortening/lengthening heat rate
L_{CE}	contractile element length
$L_{CE(OPT)}$	optimal contractile element length
m	muscle mass
S	aerobic/anaerobic scaling factor
V_{CE}	absolute contractile element velocity
$\tilde{V}_{CE}$	contractile element velocity scaled to $L_{CE(OPT)}$
$\alpha_{S(FT)}$	shortening heat rate coefficient for fast twitch fibers
$\alpha_{S(ST)}$	shortening heat rate coefficient for slow twitch fibers
α_L	lengthening heat rate coefficient

Muscle Energetics Model

In this study, the instantaneous rate of muscle metabolic energy expenditure was predicted using a modified Hill-type muscle model (Umberger et al. 2003). Total muscle energy consumption was determined from the rate of heat production and the rate at which work was done by the CE, and was computed by summing three heat rate terms with the mechanical work rate

$$\dot{E} = \dot{h}_A + \dot{h}_M + \dot{h}_{SL} + \dot{w}_{CE} \, .$$

Detailed expressions for each of these terms are provided in Umberger et al. (2003). The reader interested in implementing the present version of the muscle energy model will need to consult both the current document and the original publication (Umberger et al. 2003), which use the exact same nomenclature.

In the current study, the model formulation was changed from the original for lengthening contractions, in an effort to better account for the actual adenosine triphosphate (ATP) cost of cross-bridge cycling during eccentric muscle actions. In the original description of the model, the total energy balance was computed (Equation 18 in Umberger et al. 2003), which facilitated comparisons with some literature data (Constable et al. 1997). However, mechanical work performed *on* muscle does not appear to result in a reversal of the underlying chemical reactions that fuel muscle contraction (Woledge et al. 1985). Therefore, the actual ATP cost during lengthening should be better predicted by excluding negative CE work from the summation, and redefining the lengthening heat rate coefficient (α_L) in the model, so as to match energetic results from experimentally induced lengthening contractions measured *in vivo* (Hawkins & Molé 1997; Ryschon et al. 1997). Consistent with the original formulation, the new lengthening heat rate coefficient is still defined as a multiple of the shortening heat rate coefficient ($\alpha_{S(ST)}$), such that

$$\alpha_L = 0.3\,\alpha_{S(ST)}$$

and the total metabolic energy rate is given by if $L_{CE} \leq L_{CE(OPT)}$,

$$\dot{E} = \dot{h}_{AM}\ A_{AM}\ S + \begin{cases} \left[-\alpha_{S(ST)}\,\tilde{V}_{CE}\,(1-\%FT/100) - \alpha_{S(FT)}\,\tilde{V}_{CE}\,(\%FT/100)\right] A_S\ S - (F_{CE}\ V_{CE})/m & \text{if } \tilde{V}_{CE} \leq 0 \\ \alpha_L\,\tilde{V}_{CE}\ A\,S & \text{if } \tilde{V}_{CE} > 0 \end{cases}$$

if $L_{CE} > L_{CE(OPT)}$,

$$\dot{E} = \left(0.4\,\dot{h}_{AM} + 0.6\,\dot{h}_{AM}\ F_{ISO}\right) A_{AM}\ S + \begin{cases} \left[-\alpha_{S(ST)}\,\tilde{V}_{CE}(1-\%FT/100) - \alpha_{S(FT)}\,\tilde{V}_{CE}(\%FT/100)\right] F_{ISO}\ A_S\ S - (F_{CE}\ V_{CE})/m & \text{if } \tilde{V}_{CE} \leq 0 \\ \alpha_L\,\tilde{V}_{CE}\ F_{ISO}\ A\,S & \text{if } \tilde{V}_{CE} > 0 \end{cases}$$

where the rationale for all aspects of this expression, except the changes described above, are given in Umberger et al. (2003).

Musculoskeletal Model Parameter Values

In this study, the human body was modeled in two dimensions using seven rigid segments. These segments represented the combined head, arms, and trunk, and the right and left thigh, shank, and foot. The segment lengths, masses, center of mass locations, and moments or inertia are provided in Table A1.

Table A1. Parameters describing the model body segments.

Segment	Length (m)	Mass (kg)	CM location (m)	Moment of inertia (kg·m^2)
Thigh	0.41	10.62	0.168	0.193
Shank	0.43	3.25	0.192	0.039
Foot	0.14	1.03	0.098	0.005
Trunk	0.88	45.20	0.311	2.414

CM location is the distance from the proximal joint, or in the case for the trunk, the cranial distance from the hip joint. Foot length is distance from the ankle joint to the metatarsophalangeal joint. The trunk segment includes the mass of the arms and head.

Each actuator in the musculoskeletal model was represented using a Hill-type model of muscle contraction dynamics (Nagano & Gerritsen 2001; van Soest & Bobbert 1993), a first-order model of muscle activation dynamics (He et al. 1991), and a model of muscle energy consumption (Umberger et al. 2003). Muscle model parameter values were adopted from Umberger et al. (2006), and are provided in Table A2.

Table A2. Parameter values for the muscle model.

Muscle	Mass (kg)	Penn. (deg)	$L_{CE(OPT)}$ (m)	PCSA (m^2)	F_{MAX} (N)	L_{SLACK} (m)	WIDTH	%FT	A_{REL}	B_{REL}	τ_{ACT} (ms)	τ_{DEA} (ms)
soleus[a]	0.587	25	0.055	0.0179	3127	0.255	0.80	20	0.18	2.2	70.0	83.0
other plantar flexors[a]	0.395	10	0.039	0.0096	2389	0.349	0.56	40	0.26	3.1	60.0	71.0
gastrocnemius	0.326	14	0.055	0.0060	1384	0.376	0.61	50	0.30	3.6	55.0	65.0
vasti	2.160	4	0.086	0.0237	5925	0.148	0.55	50	0.30	3.6	55.0	65.0
rectus femoris	0.540	5	0.084	0.0061	1118	0.345	0.76	65	0.36	4.3	47.5	56.0
glutei	1.973	3	0.145	0.0128	2335	0.161	0.77	45	0.28	3.4	57.5	68.0
medial hamstrings[b]	0.905	13	0.109	0.0078	1463	0.387	0.75	35	0.24	2.9	62.5	74.0
biceps femoris long head[b]	0.351	0	0.109	0.0030	546	0.420	0.78	35	0.24	2.9	62.5	74.0
biceps femoris short head	0.262	23	0.173	0.0014	267	0.083	0.75	35	0.24	2.9	62.5	74.0
iliacus[c]	0.394	7	0.100	0.0037	704	0.091	0.74	50	0.30	3.6	55.0	65.0
psoas major[c]	0.447	8	0.104	0.0041	811	0.136	0.70	50	0.30	3.6	55.0	65.0
dorsiflexors	0.615	7	0.099	0.0059	1466	0.235	0.49	25	0.20	2.4	67.5	80.0

Penn. is muscle fiber pennation angle. $L_{CE(OPT)}$ is contractile element optimal length. PCSA is physiological cross-sectional area. F_{MAX} is contractile element maximal isometric force. L_{SLACK} is series elastic element slack length. WIDTH is the relative spread of the normalized force length curve. %FT is percentage of fast-twitch muscle fibers. A_{REL} and B_{REL} are the normalized Hill constants. τ_{ACT} and τ_{DEA} are the activation and deactivation time constants. Muscles with the same letter superscript were considered to be part of the same group, and received the same excitation signal.

The lengths of the musculotendon actuators were represented using third-order polynomials equations that were functions of the hip, knee, and ankle joint angles. The polynomials were fit to experimental tendon excursion data from the literature (Arnold et al. 2000; Németh & Ohlsén 1985; Spoor et al. 1990; Spoor & van Leeuwen 1992; Visser et al. 1990) using a least-squares approach. In cases where tabular data were not available, the relevant figures from the original articles were digitized to recover the raw data. A single equation for total musculotendon length was generated for each actuator that was a function of all three joint angles (hip, knee, and ankle). The general form of the equation was

$$L_{MT} = a_0 + a_1\theta_H + a_2\theta_H^2 + a_3\theta_H^3 + a_4\theta_K + a_5\theta_K^2 + a_6\theta_K^3 + a_7\theta_A + a_8\theta_A^2 + a_9\theta_A^3,$$

where L_{MT} is origin-to-insertion musculotendon length in m, θ_i, $i = H, K, A$ are hip, knee, and ankle joint angles in radians, and a_0 to a_9 are the polynomial coefficients. All joint angles were zero at full extension, with negative angles in the direction of hip flexion and ankle dorsiflexion, while knee flexion corresponded to positive angles. Note that for the ankle joint, zero degrees corresponded to the fully extended or plantar flexed position. Thus, the anatomically neutral position between dorsiflexion and plantarflexion would correspond to $-\pi/2$ rad (-90°). The polynomial coefficients, along with identification of the studies from which the data were obtained, are presented in Table A3. In cases where a muscle did not cross a particular joint, the appropriate polynomial coefficients were set to zero (shown as dash lines in Table A3).

Table A3. Polynomial coefficients for musculotendon length equations.

			Hip Joint			Knee Joint			Ankle Joint	
Muscle	a_0	a_1	a_2	a_3	a_4	a_5	a_6	a_7	a_8	a_9
soleus [S1]	0.280	—	—	—	—	—	—	0.093690	0.098000	0.021307
other plantar flexors [S1]	0.376	—	—	—	—	—	—	0.003370	0.012210	0.002663
gastrocnemius [S1]	0.438	—	—	—	–0.034070	0.012890	–0.003550	0.093690	0.098000	0.0213067
vasti [V]	0.188	—	—	—	0.045780	–0.007270	0.000000	—	—	—
rectus femoris [V]	0.421	0.035330	0.005920	0.000000	0.056900	–0.007940		—	—	—
glutei [N]	0.213	–0.089250	–0.021894	0.003013	—	—	—	—	—	—
medial hamstrings [N, S2]	0.432	–0.072210	0.008746	0.005905	–0.028120	–0.012593	0.005300	—	—	—
biceps femoris long head [N, V]	0.438	–0.072210	0.008746	0.005905	–0.013030	–0.005505	0.001697	—	—	—
biceps femoris short head [V]	0.258	—	—	—	–0.013030	–0.005505	0.001697	—	—	—
iliacus [A]	0.210	0.028320	0.001560	0.001650	—	—	—	—	—	—
psoas major [A]	0.260	0.028320	0.001560	0.001650	—	—	—	—	—	—
dorsiflexors [S1]	0.346	—	—	—	—	—	—	–0.012760	–0.042670	–0.011433

Author codes: A - Arnold et al. (2000), N - Németh & Ohlsén (1985), S1 - Spoor et al. (1990), S2 - Spoor & van Leeuwen (1992), V - Visser et al. (1990).

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