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Mechanics of human triceps surae muscle in walking, running and jumping

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ABSTRACT

Length changes of the muscle–tendon complex (MTC) during activity are in part the result of length changes of the active muscle fibres, the contractile component (CC), and also in part the result of stretch of elastic structures [series-elastic component (SEC)]. We used a force platform and kinematic measurements to determine force and length of the human calf muscle during walking, running and squat jumping. The force–length relation of the SEC was determined in dynamometer experiments on the same four subjects. Length of the CC was calculated as total muscle–tendon length minus the force dependent length of the SEC. The measured relations between force and length or velocity were compared with the individually determined force–length and force–velocity relations of the CC. In walking or running the negative work performed in the eccentric phase was completely stored as elastic energy. This elastic energy was released in the concentric phase, at speeds well exceeding the maximum shortening speed predicted by the Hill force–velocity relation. Speed of the CC, in contrast, was positive and low, well within the range predicted by the measured force–velocity properties and compatible with a favourable muscular efficiency. These effects were also present in purely concentric contractions, like the squatted jump. Contractile component length usually started at the far end of the force–length relation. Inter-individual differences in series-elastic stiffness were reflected in the force and length recordings during natural activity.

Keywords elasticity, force–length relation, force–velocity relation, locomotion, muscle, tendon compliance, work loop.

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A considerable amount of information is already available on the forces and power generated in common human activities like walking and running (Farley & Ferris 1998) or jumping (Bobbert *et al.* 1986). These forces and powers are generated by muscles. The present paper will concentrate upon the question how human muscles perform their task: how much of the eccentric work can be stored in the elastic components (Alexander 1988) and in what range of its force–length–velocity relation does the muscle operate in real life?

For human walking (Hof *et al.* 1983), running (Hof 1990) and jumping (Bobbert *et al.* 1986, Pandy 1990) a few modelling studies addressing these questions are available. Further experimental support for the findings in these studies is desirable, however, because several of the model parameters were derived from scaled-up animal data.

A number of studies have recently been carried out in animals: swimming fish (Rome *et al.* 1993) and jumping frogs (Lutz & Rome 1996). Closely related are measurements of muscle fibre length in humans with ultrasound (Kawakami *et al.* 1998) and animal experiments of fibre length combined with tendon force from strain gauges (Roberts *et al.* 1997, Biewener 1998).

Until now, a major problem in experiments on human muscle has been a precise determination of the series elastic properties. In intact animals or humans, muscles are always connected to limbs, with a certain mass. Because of this mass, it is difficult to move the limb fast enough to measure the complete release of the series elasticity in the short time that is available before reflexes arrive. This problem has been solved only recently for the muscles that move the human foot; strong muscles that move a limb with little mass. The

solution was a combination of a fast controlled release and extensive signal processing (Hof 1997a, b).

Our analysis is based on the three component model of the muscle–tendon complex (MTC), which can be traced back to the work of Hill (1938). In addition to a contractile component (CC), two elastic components can be identified: the parallel elastic component (PEC), parallel to the CC, and the series-elastic component (SEC) in series with CC and PEC. Both elastic components exert a force that is determined by their length, or vice versa. The force F_c generated by the CC is determined by the muscle activation (to be represented by the active state F_0), by its length l_c , and by its shortening velocity v_c . (For a list of symbols and abbreviations see the Appendix.)

All three triceps surae muscles have only short contractile fibres, with optimum lengths of 2.5–5 cm (Wickiewicz *et al.* 1983, Out *et al.* 1996, Kawakami *et al.* 1998, Lieber & Fridén 2000). This means that the SEC can largely be identified with the Achilles tendon and with the extensive aponeurosis of this muscle group, which spans the remainder of the total muscle length, some 30 cm for soleus and 40 cm for gastrocnemius (Alexander & Bennett-Clark 1977). Parallel elastic component represents mainly the elastic properties of the passive muscle fibres and of the connective tissue between them, the endo- and epimysium.

In short, our experimental method was the following. In four subjects the properties of the SEC were experimentally determined by means of the controlled-release method (Hof 1998). From the same subjects recordings were made of the ground reaction force and of the kinematics of the limbs during jumping, walking and running at several speeds. These data were used to calculate force F and total length l of the MTC of triceps surae by means of the inverse dynamics method. From the muscle force and the SEC length–force relation, SEC length l_s could be calculated. The CC length l_c is then found as:

$$l_c = l - l_s \quad (1)$$

The time course of l_c and its derivative v_c were then compared with the force–length and force–velocity relations of the CC, which had been obtained from the same subjects (van Zandwijk *et al.* 1998). The relations of force with l and l_c will be presented as F – l and F – l_c plots or work loops (Biewener 1998). In a similar way, F – v and F – v_c plots can be constructed. This approach has the advantage that the results do not depend on the degree of sophistication of the muscle model. Inverse dynamics is a well-established method, which is accurate within about 4%. The controlled-release method gives a functional measurement of the SEC force–length curve. These two methods combined suffice to construct the F – l_c and F – v_c plots that will be presented.

METHODS

Muscle model

The properties of the MTC can be expressed in terms of a muscle model. Because a detailed model of the muscle contractile properties is not necessary for our approach, the classical Hill force–length–velocity relation (Hill 1938, Zajac 1989), is adequate. In this model the force F_c of the CC is a function of CC length l_c and its first derivative, CC speed v_c . Conventionally, shortening speed is counted positive,

$$F_c = F_0 \frac{f(l_c) - mv_c/b}{1 + v_c/b} \quad (2)$$

in which F_0 is the so-called active state, the force the CC would develop at optimum length and zero velocity, and b and n are parameters. This ‘Hill relation’ holds for negative (eccentric) speed only up to the point where F_c is about $1.5F_0$; at higher negative speed F_c does not increase further (Joyce & Rack 1969). The form of (2) has been depicted in the F – v plots, e.g. in Fig 4, 8 and 10b to follow.

The function $f(l_c)$ in (2) is the normalized isometric force–length relation. For human muscle it can be determined on the basis of the sliding filament theory (Gordon *et al.* 1966) with actin and myosin filament lengths as obtained from human muscle (Walker & Schrodt 1974). A somewhat smoothed form can be fitted to this force–length relation as (Slager *et al.* 1997):

$$f(l_c) = \exp\left(-\left|\frac{(l_c/l_{ce0})^{0.545} - 1}{0.216}\right|^{2.46}\right) \quad (3)$$

The only parameter in (3) is the optimum CC length l_{ce0} , the length at which $f(l_c)$ has its maximum of 1. The force–length relation could only be measured for soleus and gastrocnemius together, with soleus dominating because of its greater strength. Assuming that $f(l_c)$ was the same for both muscles, as we did, is a simplification, because gastrocnemius has in general slightly longer muscle fibres than soleus (Out *et al.* 1996, Kawakami *et al.* 1998). The same holds for the force–velocity parameters. The SEC length l_s consists of a constant part, the ‘slack length’ l_{se0} , representing the length at zero force, and an extensible part l_{se} . According to earlier experiments (Hof 1998), l_{se} is a linear function of F for forces above a threshold force F_b ,

$$l_{se} = \frac{F + F_b}{k_1} \quad \text{for } F > F_b \quad (4)$$

The linear part is preceded by a quadratic ‘toe’ region, with

$$l_{se} = \sqrt{\frac{F}{k_2}} \quad \text{for } F < F_b \quad (5)$$

Stiffness parameter k_2 is constant, which means that the ‘toe region’ does not change shape, but the linear stiffness at high force k_1 is dependent on the active state F_0 , viz.

$$\frac{1}{k_1} = \frac{1}{k_0} + \frac{1}{c_s F_0 + k_p} \quad (6)$$

A possible interpretation is that part of the stiffness k_1 is proportional to the number of active muscle fibres, the term $c_s F_0$, with a constant common tendon stiffness k_0 in series and a residual stiffness k_p in parallel (cf. Fig. 6 of Hof 1998).

The toe and linear regions meet at $F = F_b$ such that at this point the curve has a continuous first derivative. This requires that

$$F_b = k_1^2 / 4k_2 \quad (7)$$

This representation is slightly different from the one proposed by Hof (1998), but equally well in agreement with the experimental data. For the force–length relation of the PEC, experimental curves will be given.

Total power generated by the CC is the sum of the rate of mechanical work performed, $\dot{W}_c$, and the rate of heat production $\dot{H}$. According to Hill’s original paper (1938), a contracting muscle generates an amount of heat per second equal to

$$\dot{H} = nF_0 b + nF_0 v_c \quad (8)$$

The efficiency of a muscle contraction, defined as (Woledge 1997):

$$\eta = \frac{\dot{W}_c}{\dot{W}_c + \dot{H}} \quad (9)$$

can thus be estimated as a function of v_c . This calculation does not include the efficiency of the processes leading to the phosphorylation of adenosine triphosphate (ATP), which can be assumed independent of CC speed. Equations (8) and (9) admittedly give a simplified representation of muscle thermodynamics. In the context of this paper they serve only to give an estimate of muscle efficiency as a function of shortening speed.

Subjects

All experiments were carried out on the same subjects, four healthy young men, whose relevant characteristics have been given in Table 1. From each subject informed consent was obtained according to the policy statement of the American College of Sports Medicine. The experiments consisted of three series: controlled-releases to determine the parameters of the SEC and the CC force–velocity relation, isokinetic contractions with external stimulation to determine the CC force–length relation, and recordings of ankle angle and moment in walking, running and jumping.

Controlled-release experiments

These experiments were performed on a special purpose hydraulic dynamometer for the ankle (Hof 1997a) which can generate high angular velocities. A series of isokinetic releases was performed at speeds ranging from 2 to 15 rad s^{−1} with maximum voluntary activation. The fastest releases were used to determine the SEC force–length relationship (Hof 1998), while the complete series was used for assessing the parameters of the force–velocity relation (van Zandwijk *et al.* 1998). Parameter values determined in these experiments have been given in Table 1. A controlled release at very low speed, about 0.1 rad s^{−1}, and with passive muscles, was used to measure the PEC force–length relation.

Experiments with electrical stimulation

Triceps surae was artificially stimulated for 1 s through the n. tibialis in the popliteal fossa with supramaximal pulses of 0.1 ms at frequencies of 18, 32, 24 and 20 Hz, for subjects 1–4, respectively. Ankle moment was recorded on a KinCom isokinetic ergometer (ChatteX, Chattanooga, TN, USA). Recorded were isometric contractions at angles of 80, 90, ..., 120° of plantarflexion, and isokinetic contractions at an angular velocity of 0.5 rad s^{−1}, starting with an isometric preload (van Zandwijk *et al.* 1998). These can be used to

Table 1 Subject data. Parameters of series-elastic component (SEC) elasticity, c_s , k_0 , k_p , and k_2 are from Hof (1998), his subjects 2–5, CC parameters b and n are from van Zandwijk *et al.* (1998), their subjects 4, 2, 1 and 3, respectively. Data have been transformed from angular units into linear units on the basis of an ankle moment arm of 0.05 m. For force–length parameters l_{ce0} and l_{sc0} , see Methods

Subject	Age (years)	Stature (m)	Body mass (kg)	c_s (m ^{−1})	k_0 (kN m ^{−1})	k_p (kN m ^{−1})	k_2 (MNm ^{−2})	b (m s ^{−1})	n	l_{sc0} (m)	l_{ce0} (m)
1	21	1.73	59	90	312	16	3.0	0.178	0.30	0.245	0.035
2	27	1.85	76	82	260	28	3.8	0.129	0.23	0.238	0.035
3	27	1.80	88	96	420	72	10.0	0.082	0.13	0.267	0.025
4	27	1.87	71	56	412	32	3.8	0.093	0.21	0.250	0.035
Mean		1.81	73.5	81	351	37	5.2	0.120	0.22	0.250	0.033
SD		0.05	10.4	15	68	21	3.2	0.04	0.06	0.011	0.004

estimate the (non-normalized) force–length relation, from

$$F_0 f(l_c) = F_c + \frac{v_c}{b} (F_c + nF_0) \quad (10)$$

which can be derived from (2). The advantage of electrical stimulation is that F_0 can be assumed constant among different contractions (except for a short period after the start). The CC length l_c was determined according to (1) as the difference between muscle length l and SEC length l_s . The variable part of l_s , l_{se} , can be calculated from F and the SEC force–extension curve, (4) and (5). To describe the relationship we first calculated an experimental force–length curve according to (10), the maximum of which was taken as F_0 . Subsequently, SEC slack length l_{se0} and CC optimum length l_{ce0} were chosen such that the position and width of the theoretical curve (3) for $f(l_c)$ agreed best with the experimental data.

Movement recordings

During the execution of the movements, the positions in the sagittal plane of retro-reflective markers on the subject were recorded with electronically shuttered video cameras (NAC 60/200 MOSTV, Oxford Metrics, Oxford, UK). Markers were placed at the fifth metatarsophalangeal joint, at the lateral malleolus, at the knee (on the lateral collateral ligament at the height of the joint cleft), at the greater trochanter and at the shoulder, all on the right side. Simultaneously, vertical and fore-aft components of the ground reaction force and the position of the centre of pressure were recorded with a force platform (Kistler 9281 B; Kistler Instruments, Amherst, NY, USA). Marker co-ordinates and forces were sampled at a frequency of 200 Hz. Electromyography (EMG) was also recorded, but results will not be presented here.

For running and walking a walkway of about 5 m before, and 2 m behind the forceplate was available. Subjects were instructed to walk or run at ‘slow’, ‘normal’ or ‘fast’ speed, and to look ahead instead of deliberately aiming at the forceplate. Trials were repeated until, at each speed, three recordings had been obtained in which the subject hit the forceplate correctly. Average speed was calculated from the horizontal movement of the shoulder marker. A possible change in speed during the recorded step was monitored by integrating the horizontal force component. The recorded jumps were two-legged squatting jumps. The initial posture was free, but no countermovement was allowed. The instruction was to jump as high as possible.

The ankle moment was calculated using a standard inverse dynamics approach. Because the inertia of the foot is very small, for the ankle this is practically

identical with calculating the moment from the ground reaction force times the orthogonal distance from the force vector to the ankle joint. For the (two-legged) jumping experiments, an equal contribution of both legs was assumed.

Ankle and knee angle were calculated from the two-dimensional marker co-ordinates. Prior to further processing angles were smoothed by a Blackman window with a cut-off frequency of 20 Hz.

Muscle length and force

In order to convert ankle angle to triceps surae length and ankle moment to muscle force, data from Spoor *et al.* (1990) have been used, which were obtained from tendon position measurements in two cadavers. The data for the Achilles tendon can be used to estimate the length of the soleus. An adequate fit was

$$l_{\text{soleus}} = 0.05 \cos \varphi + 0.30 \quad (11)$$

in which ϕ is the ankle plantarflexion angle in radians, between tibia and foot sole (erect position is $\pi/2$ rad). Gastrocnemius length is dependent on both ankle angle ϕ and knee flexion angle ψ (with zero degrees corresponding to full extension) and could be fitted as

$$l_{\text{gastroc}} = 0.05 \cos \varphi + 0.0069(\psi - 0.9)^4 - 0.02(\psi - 0.9) + 0.410 \quad (12)$$

Triceps surae force was found from the ankle moment as $F = M/d$. The moment arm d with respect to the ankle follows from differentiation of (11) or (12) with respect to ϕ :

$$d = 0.05 \sin \varphi \quad (13)$$

In the above, a length for soleus of 0.30 m and for gastrocnemius of 0.40 m has been assumed in the erect standing position, with $\psi = 0$ and $\varphi = \pi/2$. As a consequence, it has been assumed that SEC slack length l_{se0} for gastrocnemius is 0.10 m longer than for soleus. It has not been attempted to correct muscle lengths or moment arms to the size of the subjects. There are insufficient anatomical data available to justify such a refinement, and it would only hinder a comparison between subjects in the present study.

In the Results, MTC length will be given as $l - l_{se0}$. This will yield lengths of about the same magnitude as $l_c = l - l_{se0} - l_{se}$, which makes comparisons easier. Force from the PEC was small in all cases, therefore in most cases total force F will be presented, instead of $\bar{F}_c$.

It should be borne in mind that the inverse dynamics method, as applied here, can only give the net moment around the ankle, and cannot differentiate between the contributions because of forces from the separate heads of triceps surae, nor detect to what

degree a cocontraction of tibialis anterior has been present. In this paper, it was assumed that muscle force was divided over soleus and gastrocnemius in the constant proportion 2 : 1. This is in agreement with the average ratio of physiological cross-sections (Out *et al.* 1996), but does not take into account that the activations of the muscles or their force–length and force–velocity relations might have been different (Lieber & Fridén 2000). Effects of tibialis cocontraction were reduced by presenting in the muscle force curves only those parts corresponding to positive moments.

The peak value of the active state F_0 was estimated by fitting the Hill relation (2) to the experimental F – v_c plot. This F_0 value was also used in the calculation of SEC stiffness k_1 (6) and the presented force–length relations.

RESULTS

Force–length relation

An example of an experimental force–length relation has been presented in Figure 1. Subject was no. 2, with a SEC stiffness around average, who will serve as an example in most results to follow. On the right the force–length data have been plotted as a function of MTC length ($l - l_{se0}$). The isometric contractions (with $v_c = 0$) at 80, 100 and 120° of plantarflexion, gave one data point (×) each. The data from the isokinetic contraction, thin dashed line, were calculated according to (10). It can be seen that the isokinetic movement was preceded with an isometric phase at the initial angle of about 80°. For the data on the left, the cor-

Figure 1 The CC force–length relation for subject 2. Data measured for the muscle–tendon complex (MTC) are in the right panel: (×) is data of isometric contractions at angles of 80, 100 and 120° of plantarflexion; thin dashed line: data from an isokinetic contraction with electrical stimulation at 0.5 rad s^{−1}. Top scale: ankle angle corresponding to length scale for $l - l_{se0}$ below. The left panel presents the data after correction for stretch of the SEC: (○) isometric contractions, drawn thin line: isokinetic contraction, thick dashed line: force–length relation fitted to the experimental data. The force–length curve $F_p(l_c)$ of the parallel elastic component (PEC) is also shown.

rection for SEC shortening has been applied, (○) and continuous line. The experimental data could be fitted by a force–length relation (3) with $l_{ce0} = 3.5$ cm, $l_{se0} = 23.8$ cm and $F_0 = 3900$ N (thick dashed line). Parameters for all four subjects are presented in Table 1. It should be noted that the force–length relation as found here refers to all three heads of triceps surae taken together.

Running

The recordings of running gave the most complete picture of the effects of series elasticity on muscle action. The results will again be presented for subject 2 in a recording of fast running at a speed of 3.7 m s^{−1}.

Figure 2a gives the ankle moment and angle. The ankle moment curve had a single peak with a total duration of 200 ms and a peak value of 215 Nm. Subject 2 was a ‘rearfoot striker’ (Cavanagh & LaFortune 1980), i.e. he touched the floor heel first. The other three subjects were ‘midfoot strikers’: they showed an earlier rise of the moment, immediately after heel strike.

Figure 2 Fast running, subject 2, at speed of 3.7 m s^{−1}. Time of heel contact (RHC) and toe-off (RTO) have been indicated with vertical dashed lines. (a) Ankle moment and (b) ankle angle (in radians, neutral foot position is 1.57 = 90°) and knee flexion angle. Angle recordings have not yet been smoothed.

Peak moment varied considerably among subjects, from 145 Nm in subject 4 to 266 Nm in subject 3 (see Table 2). Within each subject, peak moment increased on the average slightly with running speed, in subject 2 from 185 Nm at 2.9 m s⁻¹ to 215 Nm at 3.7 m s⁻¹.

Ankle angle (Fig. 2b) showed a dorsiflexion followed by a plantarflexion movement. The knee angle had a similar flexion-extension sequence, but with extension starting slightly earlier. As could be observed from the kinematic data, this was because in running two motions could be discerned. One is a shortening-lengthening of the leg, giving flexion-extension in ankle, knee and hip. The other is the forward movement, giving hip and knee extension, but ankle dorsiflexion. Maximum dorsiflexion of the ankle and peak ankle moment occurred almost simultaneously, within 10 ms, for all running recordings.

Soleus muscle force has been plotted against soleus MTC length (F - l plot or work loop) in Figure 3a. In agreement with the dorsi-plantarflexion movement, MTC action was first eccentric, then concentric. In this recording, 21 J of energy was absorbed by the MTC in the eccentric phase and 54 J of work was performed by the soleus MTC on the ankle in the concentric phase. These values could be calculated from the areas below the ascending and descending part of the curve, respectively.

The curve for l_c , obtained by subtracting SEC stretch l_s from MTC length l follows quite a different pattern (Fig. 3a). For the CC the complete contraction is concentric: the increasing stretch of the SEC caused by the rise in muscle force in the first part of the contraction more than offsets the lengthening of the complete MTC. In the second part, with declining

Table 2 The muscle-tendon complex (MTC) work and CC work. One representative example is given for all subjects and all movement conditions. From left to right: subject, average speed; Δv , change of speed during the step (determined from horizontal ground reaction force, see Methods); $M_{\max}$, peak ankle moment; F_0 , peak active state; W^- , W^+ , negative and positive work of total MTC; sum = $W^- + W^+$, W_c^- , W_c^+ , work performed by the contractile component. Results for soleus and gastrocnemius have been given, assuming that muscle forces were in the proportion of 2 : 1. When the storage of elastic energy in the series elastic component works ideally, $W_c^+ = W^- + W^+$ and $W_c^- = 0$ when $W^- + W^+$ is positive. When this sum is negative, in landing after a jump, $W_c^- = W^- + W^+$ and $W_c^+ = 0$, see Hof (1990)

	Subject	Speed (m s ⁻¹)	Δv (m s ⁻¹)	$M_{\max}$ (N m)	Soleus						Gastrocnemius						
					F_0 (N)	W^- (J)	W^+ (J)	Sum (J)	W_c^- (J)	W_c^+ (J)	F_0 (N)	W^- (J)	W^+ (J)	Sum (J)	W_c^- (J)	W_c^+ (J)	
Slow walking	1	1.08	0.10	80	1500	-6	12	6	0	6	800	-6	9	3	-2	6	
	2	1.32	-0.02	97	1500	-3	16	13	0	14	600	-3	12	10	0	12	
	3	1.48	-0.06	145	3000	-8	22	14	-1	16	1500	-5	12	7	0	10	
	4	0.64	-0.11	65	1200	-4	2	-1	-1	0	600	-1	2	1	0	2	
Normal walking	1	1.25	-0.07	83	1500	-5	13	8	0	8	800	-5	9	3	-2	6	Figures 9 and 10
	2	1.51	0.06	102	2500	-1	22	21	0	22	1500	-2	15	13	0	15	
	3	1.92	-0.09	136	7000	-7	29	22	0	24	3500	-6	14	8	-3	12	
	4	1.01	-0.15	81	1500	-3	8	5	0	5	1000	-3	7	4	0	6	
Fast walking	1	1.95	-0.10	88	2300	-2	16	14	0	14	1200	-4	10	5	-3	10	
	2	1.97	0.12	135	3500	-1	23	21	0	23	2500	-3	19	16	0	18	
	3	2.26	-0.12	166	8000	-7	31	23	-4	29	4000	-7	16	9	-5	16	
	4	1.64	0.01	101	3000	-3	16	12	0	13	1500	-4	11	7	-1	9	
Slow running	1	2.97	0.16	153	4500	-27	38	11	-3	17	2300	-11	14	3	0	6	Figure 11a
	2	2.88	0.12	185	6000	-14	47	33	0	37	3000	-8	19	11	0	17	
	3	3.93	-0.03	248	10 000	-33	44	11	0	15	3000	-14	16	2	0	6	
	4	2.68	-0.15	117	4000	-12	20	9	0	11	1200	-7	7	0	0	6	
Fast running	1	3.91	0.14	163	4500	-40	40	1	-13	16	2300	-16	14	-2	-1	2	Figure 5
	2	3.69	0.11	215	7000	-21	54	32	0	38	3500	-11	20	10	0	14	
	3	5.39	0.00	266	16 000	-45	66	21	-2	27	8000	-19	22	3	0	8	Figure 11b
	4	3.63	0.12	145	8000	-19	29	10	0	13	1500	-10	10	-1	0	2	
Jump up	1			79	6000	-1	30	29	0	28	1200	-1	7	7	0	8	Figures 6–8
	2			107	4200	-1	28	27	0	25	1200	-1	7	6	0	6	
	3			139	14 000	-2	53	51	-1	51	2500	-1	12	11	0	11	
	4			99	3500	0	36	36	0	34	1300	0	8	7	0	7	
Jump landing	1			91	800	-40	2	-38	-36	0	400	-15	0	-15	-14	0	
	2			154	2000	-31	14	-17	-7	0	1000	-10	13	3	-1	8	
	3		na														
	4			147	1400	-51	13	-38	-34	1	1800	-18	6	-12	-10	0

Figure 3 F - l_c and F - l plots for subject 2, running at 3.7 m s^{-1} , same recording as Fig. 2. (—) Muscle force F as a function of CC length l_c ; (- . - .) F as a function of total muscle-tendon length minus slack length $(l - l_{se0})$; (- - -) force-length relation, with $l_{ce0} = 3.5 \text{ cm}$. With length and force calculated (a) for soleus, $F_0 = 7000 \text{ N}$ and (b) for gastrocnemius, $F_0 = 3500 \text{ N}$. Time proceeds in the direction of the arrows.

force, CC shortening is much less than MTC shortening. A consequence is that negative CC-work is virtually nil and that positive CC work, equal to the area below the F - l_c curve, is much less (38 J) than positive MTC work. Data on MTC and CC work for all subjects and speeds have been given in Table 2.

The CC force-length relation has been given in the figure for comparison, with $F_0 = 7000 \text{ N}$ estimated from the F - v_c curve to follow. It is seen that CC length started at the far end of the force-length relation and traversed mainly the descending limb. In part of the recordings, with decreasing force, little shortening occurred and CC length stayed close to optimum.

The difference between MTC and CC movement was also evident when soleus force was plotted against soleus velocity (Fig. 4a). While the MTC showed a considerable speed variation, from lengthening at 0.25 m s^{-1} to shortening at more than 0.6 m s^{-1} (well above the maximum CC shortening speed), CC shortened at a steady pace between 0.1 and 0.2 m s^{-1} , in both the rising and falling phase. Hill's force-velocity relation (2) fitted with F_0 , has been given in the figure. Although F_0 is in reality not constant, the experimental

Figure 4 The F - v_c and F - v plots for subject 2, running at 3.7 m s^{-1} , same recording as Figures 2 and 3. (-o-o-o-) Muscle force F as a function of CC-speed v_c . Time between symbols 5 ms. (-+--++) F as a function of MTC speed v ; (- - -) Hill force-velocity relation, Equation (2). (a) Soleus, $F_0 = 7000 \text{ N m}$. Thin drawn line: η , efficiency of muscle contraction (η) as a function of v_c , right hand scale; (b) gastrocnemius, $F_0 = 3500 \text{ N m}$.

F - v_c loop keeps close to the Hill curve for a considerable part of the contraction.

The efficiency, calculated according to (9), has been also been plotted in Fig. 4a for subject 2. Maximum efficiency for soleus in this subject occurred at $v_c = 0.075 \text{ m s}^{-1}$, but efficiency was over 90% of the maximum for quite a wide range of v_c , from 0.03 to 0.15 m s^{-1} .

Figures 3b and 4b give the F - l and F - v plots for gastrocnemius. The F - l and F - l_c plots are slightly different from soleus, because gastrocnemius length is also dependent on knee angle. The F - v_c recording (Fig. 4b) shows that gastrocnemius v_c varied more; it was higher in the phase before peak force, and lower than soleus v_c afterwards.

Figure 5 shows F - l plots for a step from subject 1, an experienced distance runner, in which negative and positive work were about the same, 40 J for soleus and 15 J for gastrocnemius. The F - l loop was quite narrow for soleus (Fig. 5a). For gastrocnemius (Fig. 5b) this was even more so: l_c was almost constant during the whole contraction. The CC did not shorten or lengthen at all, and its length was close to the optimum of the force-length relation. This is reflected in very low

values for gastrocnemius CC-work: $W_c^- = -1$ J and $W_c^+ = 2.3$ J (Table 2). For soleus the effect is less evident: $W_c^- = -13$ J and $W_c^+ = 16$ J.

The findings for l_c in the other subjects followed a similar pattern. In all cases studied, peak force was generated with l_c around the optimum. When the difference between negative and positive work was big, and thus a considerable CC shortening was involved, l_c started at the long end of the force–length relation, 1.4 – $1.8 \times l_{ce0}$ and shortened unto a length at or shortly below optimum, 0.9 – $1.0 \times l_{ce0}$. An exception was subject 3, who had a l_{ce0} of 2.5 cm only. In his case shortening went on to lengths of about $0.6 l_{ce0}$.

The CC shortening speed around the maximum force showed a similar pattern as well: soleus v_c varied in all subjects in a narrow range around the optimum, 0.05 – 0.1 m s⁻¹. Gastrocnemius v_c was on average even lower, around zero.

Table 2 gives values for MTC and CC work for a representative sample of running recordings for all subjects. In all cases the pattern was: a considerable W^- , a higher W^+ , a negligible W_c^- and a W_c^+ about equal to $(W^+ + W^-)$.

Figure 5 The F – l_c and F – l plots for subject 1, fast running, 3.6 m s⁻¹. (—) Muscle force F as a function of CC length l_c ; (– · –) F as a function of total muscle–tendon length minus slack length $(l - l_{se0})$; (– – –) force–length relation, with $l_{ce0} = 3.5$ cm. (a) Soleus, $F_0 = 4500$ N and (b) gastrocnemius, $F_0 = 2250$ N.

Jumping

The recorded jumps were two-legged squatting jumps: subjects started from a squatting position, with strongly dorsiflexed ankles and flexed knees and hips. In the initial position the ankle moment was around 40 Nm (Fig. 6) in an isometric contraction. At push-off the ankle moment increased up to 105 Nm. After the peak it swiftly decreased to zero in the flight phase. Subject 2 landed on his forefeet, reaching finally a squatted posture again.

The events in take-off and in landing were quite different. The F – l plot for take off (Fig. 7a) shows that rotation of the ankle, and MTC lengthening, started only when the moment had about reached its maximum. The F – l_c plot started from a point on the descending limb of the force–length relation, but now it traversed the greater part of it. The F – v_c plot (Fig. 8) shows that, except at the isometric start and at the very end of the movement, v_c was positive. It rose to 0.1 – 0.15 m s⁻¹, similar to running. The landing in this subject was an almost perfect elastic bounce for soleus: moment and MTC length both oscillated, but l_c hardly changed (Fig. 7b). In the other subjects, and in the gastrocnemius of the present subject, a partly eccentric contraction was seen at landing, with l_c lengthening.

Walking

Ankle moment and angles for subject 2 walking at the moderate speed of 1.51 m s⁻¹ have been given in

Figure 6 Two-legged squatting jump, subject 2. Time of toe-off and touch-down have been indicated with vertical dashed lines. (a) Ankle moment for right leg and (b) ankle and knee angle.

Figure 7 Two-legged squatting jump, subject 2, same recording as Fig. 6. F – l_c and F – l plots. Soleus muscle. (—) Muscle force F as a function of CC length l_c ; (– – –) F as a function of total muscle–tendon length minus slack length ($l - l_{se0}$); (– · – ·) force–length relation, $l_{ce0} = 3.5$ cm. (a) Take-off, $F_0 = 4200$ N and (b) landing, $F_0 = 3000$ N.

Figure 8 Take-off phase of two-legged squatting jump, subject 2, soleus (same recording as Figs 6 and 7a). F – v_c and F – v plots. (–o–o–o–) Muscle force F as a function of CC speed v_c . Time between symbols is 5 ms. (–+–+–+) F as a function of MTC speed v ; (– · – ·) Hill force–velocity relation (Equation 2) with $F_0 = 4200$ N.

Figure 9. In this subject the moment was negative for a short time after heel contact, which could be attributed to the action of the tibialis anterior muscle by inspection of the EMG. The positive part of the moment curve usually had a bimodal shape, with the second peak, at push-off, being the highest. Peak moment at this speed was about half that found in running, in the present case 102 Nm vs. 210 Nm in fast running, and

Figure 9 Subject 2, walking at a normal speed of 1.51 m s^{-1} . (a) Ankle moment for right leg and (b) ankle and knee angle. Time of heel contact (RHC) and toe-off (RTO) have been indicated with vertical dashed lines.

increased with speed (see Table 2). Knee angle (Fig. 9b) followed a similar pattern as in running (Fig. 2b) but with smaller amplitude. Maximum ankle dorsiflexion was considerably less, around 1.4 rad or 80° , and the minimum angle occurred later. As a result, length changes of gastrocnemius and soleus were less different than in running.

The pattern of the F – l_c plots (Fig. 10a), started at the long end of the force–length relation, as in running, force reached a maximum at optimum length, and decreased with little change of l_c . A difference with running is that in walking the measured W^- was small compared with W^+ (Table 2), the loops were thus wider. The F – v_c plot (Fig. 10b) shows again that when force was high, CC speed was lower than in running, between 0 and 0.1 m s^{-1} .

DISCUSSION

It is evident from the Results that, because of SEC compliance, CC length changes are very different from whole muscle length changes. This may indeed be expected in a muscle, where maximal SEC extension, 4.5 cm in running (Fig. 3a, b), is more than the complete muscle fibre (CC) length of about 3.5 cm . The results are in agreement with studies in which muscle fibre length could be measured directly by means

Figure 10 Subject 2 walking, same recording as Fig. 9. (a) The $F-l_c$ and $F-l$ plots for soleus. (—) Muscle force F as a function of CC-length l_c ; (---) F as a function of total muscle-tendon length minus slack length ($l - l_{se0}$); (- - -) force-length relation, with $l_{ce0} = 3.5$ cm and $F_0 = 2500$ N. (b) The $F-v_c$ and $F-v$ plots for soleus. (-o-o-o-) Muscle force F as a function of CC-speed v_c . Time between symbols 5 ms. (-+-+ -) F as a function of MTC speed v . (- - -) Hill force-velocity relation (2) with $F_0 = 2500$ N. The curves have been traversed in the direction of the arrows.

of ultrasound (Griffiths 1989, Roberts *et al.* 1997, Kawakami *et al.* 1998), with calculations (Alexander & Bennett-Clark 1977), and with model simulations for human muscles (Hof *et al.* 1983, 1990). The argument can be summarized by differentiating (1) and applying the definition of elasticity. This gives:

$$v_c = v + \frac{1}{k_1} \frac{dF}{dt} \quad (14)$$

In walking and running there is a sequence of first negative v and an increase of F (eccentric phase) followed by a positive v and a decrease of F , in the concentric phase. As a result the amplitude of fluctuations in CC speed v_c is much smaller than that in v , the shortening speed of the complete MTC.

The results on running and walking confirm earlier estimates on the importance of elastic energy storage (Cavagna 1977, Alexander 1988, Hof 1990). The energy saving in eccentric-concentric actions can be illustrated by multiplying (14) with F and integrating over the complete contraction (Hof 1990). This gives:

$$W^- + W^+ = W_c^- + W_c^+ \quad (15)$$

The algebraic sum of negative and positive MTC work in a complete contraction is equal to the work performed by the CC. The W and W_c correspond to the areas under the curves of the $F-l$ and $F-l_c$ plots, respectively. Except for small areas at the start or the end of the movement, all $F-l_c$ plots we saw were traversed from right to left (as in Figs 3, 5, 7, 10 and 11). This means that W_c^- was very small, a few Joules or less, and thus the required compensation by W_c^+ minimal. This can be verified from Table 2. Eccentric-concentric contractions can thus be performed very efficiently by muscles with a compliant tendon. An exception was the behaviour in landing after a jump. In that case the dissipation of energy is an obvious task for the muscle.

In the example of running in Figure 5 this mechanism stood out very clearly. The W^- and W^+ for soleus were both about 40 J, their sum was thus zero and W_c^+ was much smaller, about 16 J for soleus and for gastrocnemius no more than 2 J. In the latter case muscle can be compared with a perfectly elastic 'bouncing ball' (Cavagna 1977).

From the muscle actions presented, running shows this 'elastic energy storage' effect most clearly: in Table 2 most values of W_c^- are close to zero. In the push-off of the squatting jump, all work carried out by the MTC is concentric, storage of negative work is thus not possible. Even then a compliant tendon is helpful, however (Fig. 7a). First, a considerable shortening of the CC (and thus a production of work) already takes place in the isometric phase, when the force increases but the ankle is not yet plantarflexing. The CC thus can do more work because there is more time. Secondly, CC shortening takes place at a lower – and more efficient speed than that of the whole MTC (Fig. 8). These effects are known as the 'catapult effect' (Alexander & Bennett-Clark 1977). Running and walking show this catapult effect as well. It explains why MTC speeds can well exceed the maximum shortening speed of the CC, which for triceps surae is around 0.5 m s^{-1} (Figs 4 and 8).

It should be stressed that the results presented apply to triceps surae only. In running at moderate speeds, W^+ in triceps surae is for most subjects greater than W^- , while the reverse is the case in, e.g. quadriceps femoris (Winter 1983). Thus, in quadriceps femoris some of the negative work cannot be recovered by elastic energy storage and gets lost. One might suspect that part of the different values for W^+ and W^- might have been related to acceleration or deceleration during the step. In many recordings (Table 2) speed was indeed not constant, but a systematic effect on $(W^+ + W^-)$ could not be found.

Limitations of the method

Two sources of error may have influenced the presented F – l and F – v loops: ankle moment and angle measured in the movement, and the moment–angle relation of the SEC, determined by the controlled release.

Ankle moment has been determined by means of the well-established inverse dynamics method. For the ankle the moment is mainly determined by the moment of the measured ground reaction force with respect to the ankle axis. The distance between ankle marker and force vector can be estimated with an accuracy of about 5 mm. This corresponds to an error of about 4% in moment and force. The ankle angle, which has been derived from the kinematic data (cf. Fig. 2b) contained some noise, of the order of 0.02 rad, which made smoothing necessary before differentiation. The corresponding error in MTC length was about 1 mm. The error in the moment in controlled release experiments was shown (Hof 1997b) to be of the order of 5–8 Nm, the error in the angle was less than 1°. Taken together with the 4% error in the moment and with the average SEC stiffness, the resulting error in CC length was estimated at 4 mm.

An unavoidable limitation of inverse dynamics is that soleus and gastrocnemii cannot be separated. It was therefore assumed that soleus and gastrocnemius force was shared among the muscles in a fixed proportion, which we assumed to be 2 : 1 (Out *et al.* 1996). In reality, however, the sharing of the muscle forces and their time courses, may well have been different. Only around maximum force, one can reasonably assume that muscle forces will be proportional to physiological cross-sections.

Triceps surae and the antagonist tibialis anterior cannot be separated either. The EMG recordings show that in walking and running cocontraction is present at the beginning of stance. During walking, in the subject presented, antagonist activity resulted even in a negative moment over a short period (Fig. 10a). A consequence is that in reality triceps surae force has been higher than calculated from inverse dynamics. This means that the reported amount of negative MTC work might have been underestimated.

For the sake of presentation, the measured moments have been converted to muscle force, and the angles to muscle length. The moment arm for the ankle, which is the essential factor in this conversion (11)–(13), has been assumed to be 5.0 cm at the neutral position. This does not take into account the differences between subjects. There are additional uncertainties. It was recently observed (Maganaris *et al.* 1998) that triceps surae moment arm can increase 22–27% when going from rest to maximum voluntary contraction (MVC),

because the muscles become thicker. The ankle axis is not perfectly perpendicular to the sagittal plane, and therefore the ankle moment can be overestimated 6–22% (Scott & Winter 1991). An increase of the moment arm above 5 cm would result in a proportional increase in the lengths and velocities, but at the same time in a proportional decrease in force. Therefore, energy and work would not change, nor would the general form of the F – l and F – v curves or the general findings on energy conservation and efficiency.

It cannot be excluded that a minor systematic difference in the determination of the absolute ankle angle has occurred between the kinematic recordings and the ergometer data. This may explain why F – l_c plots and force–length relations are in good, but not perfect agreement.

Peak values for the active state F_0 were obtained by fitting the Hill relation (2) to the experimental F – v_c plots. Remarkably high values were found (see Table 2), especially in fast running. The maximum muscle forces in running are already considerably (25–80%) higher than the values in isometric MVC, which amounted to 1360, 1640, 2300 and 1550 N for soleus in subjects 1–4, respectively. As a consequence of the Hill force–velocity relation, values of active state F_0 are 1.5–2 times the peak force. This results in a considerable discrepancy between the F_0 determined from the isometric MVC and the F_0 assessed from peak force in running. This suggests that, at least in triceps surae, maximum activation is not attained in MVC. A related finding (Hof *et al.* 1983) is that EMG levels can be considerably higher in running or jumping, than in isometric MVC.

In the above it should be kept in mind that the determination of F_0 has an estimated error of about 20%. These errors in F_0 have some influence on the estimate of SEC stiffness k_1 (6).

Force–length properties

In our representation the width of the force–length relation is determined by the parameter l_{ce0} , the CC length for maximal force. We found values for l_{ce0} which may seem quite short, 2.5 or 3.5 cm (± 0.5 cm), but which are in agreement with anatomical data. The number of sarcomeres per fibre for the relevant muscles have been determined by Wickiewicz *et al.* (1983). Assuming a sarcomere length for maximal force of 2.7 μ m (Walker & Schrodt 1974) this results in values for l_{ce0} of 3.8, 4.1–4.3 and 5.1–8.1 cm for soleus, gastrocnemius medial head and gastrocnemius lateral head, respectively.

In a recent study (Kawakami *et al.* 1998) fascicle lengths and pennation angles in human triceps surae were measured by ultrasound, both in passive muscle

and during maximal isometric contractions. It should be kept in mind that our data on CC-length are effective lengths, equal to fascicle length $\times \cos(\text{pennation angle})$. The values of Kawakami *et al.* (1998) for CC-length in gastrocnemius medialis are in good agreement with our calculations on the isometric data of Fig. 1, on the understanding that their measured lengths were shorter in soleus and longer in gastrocnemius lateralis than our predictions. This stresses once more that our experimental muscle parameters are in fact weighted averages of three muscles with different properties. The SEC 'slack length' l_{se0} determines the position of the force-length relation relative to the ankle angle. Because of the narrowness of the force-length relation, it could be estimated quite accurately (± 2 mm). There were significant differences between subjects. This is reflected in the calculated angles at which the moment-angle relation is maximal. These angles ranged from 99° of plantarflexion in subject 3 (Fig. 11a) to 123° in subject 2 (Fig. 1).

A general finding was that at the onset of the action, l_c was near the end of the descending limb of the force-length relation. This finding is in contradiction with the findings in literature that semimembranosus of jumping frogs (Lutz & Rome 1996), cat ankle flexors (Goslow *et al.* 1973, 1977) and cat peroneus longus (Eerbeek & Kernell 1991) operate around the maximum or on the ascending limb of the force-length relation. It should be noted that these findings are from muscles with relatively long fibres, wide force-length relations, and little stretch of the SEC. In human triceps surae, with its short fibres and compliant SEC, the situation is different. The ankle joint range of movement is about 60 – 120° of plantarflexion. This corresponds to a length range of the MTC of about 5 cm, equal to the full range of the CC force-length relation (see Fig. 1). It seems thus logical that contractions should start at the long end of the CC force-length relation. A second reason is that at a moderate level of force the SEC is already stretched some 4 cm. Contraction thus should start at long CC lengths if they are to end at a CC length at which some force can still be developed (see the isometric data in Fig. 1). It is efficient as well: for a muscle that has to perform the maximum amount of CC work (W_c^+), the greatest possible CC shortening should be exploited. An example is the jump take-off of Fig. 7a.

Variations in stiffness

The SEC stiffness parameter k_1 showed considerable differences, among subjects and within the same subject at various levels of muscle activation. Both were reflected in the kinematic registrations. Figure 11a shows the $F-l$ and $F-l_c$ plot for fast running in subject

Figure 11 Variation in SEC stiffness. (a) $F-l$ (— · — · —) and $F-l_c$ (thin continuous line) plots of running at 3.93 m s^{-1} in subject 3. The SEC stiffness parameter k_1 was 330 kN m^{-1} , in agreement with the measured values of Table 1 and $F_0 = 10\,000 \text{ N}$. $F-l_c$ plot (thin dashed line) when the stiffness parameters and $F_0 = 8000 \text{ N}$ of subject 4 are used, which gives $k_1 = 260 \text{ kN m}^{-1}$. (b) $F-l$ (— · — · —) and $F-l_c$ (thin continuous line) plots of running at 3.63 m s^{-1} in subject 4. The SEC stiffness parameter k_1 was 260 kN m^{-1} , in agreement with the measured values of Table 1 and $F_0 = 8000 \text{ N}$. $F-l_c$ plot (thin dashed line) with $k_1 = 107 \text{ kN m}^{-1}$, corresponding to the same stiffness parameters, but with $F_0 = 1300 \text{ N}$, the value found in slow walking. Note that the toe region of the SEC is not changed with a change of F_0 . In both figures the force-length relation has also been drawn (thick dashed line).

3, the subject with the highest stiffness. As in Figure 5, MTC length changes and muscle force were nicely matched, so that a minimum amount of CC work had to be performed. When instead of the correct stiffness for subject 3, the much lower stiffness of subject 4 was used for the SEC of subject 3 (thin dashed line in Fig. 11a), an evident overcorrection resulted.

Subject 4 had not only the lowest stiffness, but also the greatest variation in stiffness with muscle activation (a low a_k , see Table 1). Figure 11b gives the $F-l_c$ plot for running in this subject, which shows an efficient contraction, with hardly any negative CC-work. When the stiffness in running ($F_0 = 8000 \text{ N}$) was set equal to that in slow walking ($F_0 = 1300 \text{ N}$), a minor overcorrection resulted (dashed line in Fig. 11b).

A comparison of Figure 11a, b shows that subjects 3 and 4 adapted to their different stiffness. The range of

ankle motion was similar, going from 90 to 70 to 110°, but maximal soleus force in the 'stiff' subject 3 (3550 N) was almost twice as high as in subject 4 (1930 N). This ratio could not be explained by the difference in their body masses, 88 vs. 77 kg.

CONCLUSION

The human triceps surae muscle group comprises muscles with short fibres and long tendons and aponeuroses. The amount of stretch of the SEC at high forces is comparable in size with the shortening range of the CC and the MTC length changes during activity. As a result, the history of the CC length change during a contraction is completely different from that of the total MTC, as reconstructed from the joint angle.

In eccentric–concentric contractions, like in walking or running, the negative MTC work performed in the eccentric phase is completely stored as elastic energy. This elastic energy can be released in the concentric phase, at speeds well exceeding the maximum shortening speed predicted by the Hill force–velocity relation. The CC speed, in contrast, is positive and low, well within the range predicted by the measured force–velocity properties, and compatible with a favourable muscular efficiency. These effects on CC speed are also present in purely concentric contractions, like the squatted jump. Differences in SEC stiffness between subjects are reflected in their ankle moments, 'stiff' subjects showing a higher peak ankle moment.

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APPENDIX

Nomenclature

- b (m s^{-1}) velocity constant in Hill relation (2)
- CC contractile component
- c_s (m^{-1}) constant in SEC equation (6)
- d (m) moment arm of triceps surae with respect of the ankle
- $f(l_c)$ normalized force–length relation (3)
- F (N) total muscle force = $F_c + F_p$
- F_b (N) force level at which the toe region of the SEC changes into the linear part (4, 5)
- F_c (N) force developed by the contractile component
- F_p (N) force developed by the parallel elastic component
- F_0 (N) active state, the force the CC would develop at zero velocity and at the maximum of the force–length relation
- $\dot{H}$ (W) rate of muscle heat production (8)
- k_p (Nm^{-1}) constant in SEC equation (6), residual stiffness at $F_0 = 0$

- k_0 (Nm^{-1}) constant in SEC equation (6), tendon stiffness
- k_1 (Nm^{-1}) stiffness of linear part of SEC (6), depends on F_0 , see (6)
- k_2 (Nm^{-2}) stiffness of quadratic part of SEC (toe region) (5)
- l (m) total length of muscle–tendon complex, distance from origo to insertion. To facilitate a comparison with l_c , in the figures $l - l_{se0}$ has been given, MTC length minus slack length
- l_c (m) length of contractile component = length of muscle fascicles
- l_{ce0} (m) CC length at which muscle force is maximal, parameter of force–length relation (3)
- l_s (m) total length of series elastic component $l_s = l_{se0} + l_{se}$
- l_{se} (m) extension of series elastic component
- l_{se0} (m) constant part of series elastic component length, ‘slack length’
- M (Nm) moment of triceps surae muscle with respect to the ankle $M = Fd$
- MTC muscle–tendon complex
- MVC (isometric) maximum voluntary contraction
- n constant in Hill relation, defines maximum CC velocity v_0 by: $v_0 = b/n$
- PEC parallel elastic component
- SEC series elastic component
- v (m s^{-1}) shortening speed of muscle–tendon complex = $-d/dt$
- v_c (m s^{-1}) shortening speed of contractile component = $-dl_c/dt$
- $\mathcal{W}$ (J) mechanical MTC work = $\int F dl = \int F v dt$
- $\mathcal{W}^+$ (J) positive or concentric MTC work, as $\mathcal{W}$ but with $v > 0$
- $\mathcal{W}^-$ (J) negative or eccentric MTC work, as $\mathcal{W}$ but with $v < 0$
- $\mathcal{W}_c$ (J) work performed by the contractile component = $\int F_c v_c dt$
- $\mathcal{W}_c^+$ (J) positive CC work, as $\mathcal{W}_c$, but only for $v_c > 0$
- $\mathcal{W}_c^-$ (J) negative CC work, as $\mathcal{W}_c$, but only for $v_c < 0$
- $\dot{\mathcal{W}}$ (W) mechanical power, work per unit time, = Fv
- η efficiency of muscular contraction (9)
- φ (rad) ankle angle = $\pi/2$ in neutral position, increases with plantarflexion
- ψ (rad) knee flexion angle = 0 with fully extended knee