

MECHANICAL POWER AND WORK OF CAT SOLEUS, GASTROCNEMIUS AND PLANTARIS MUSCLES DURING LOCOMOTION: POSSIBLE FUNCTIONAL SIGNIFICANCE OF MUSCLE DESIGN AND FORCE PATTERNS

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Summary

Electrical activity, forces, power and work of the soleus (SO), the gastrocnemius (GA) and the plantaris (PL) muscles were measured during locomotion in the cat in order to study the functional role of these ankle extensor muscles. Forces and electrical activity (EMG) of the three muscles were measured using home-made force transducers and bipolar, indwelling wire electrodes, respectively, for walking and trotting at speeds of 0.4 to 1.8 ms⁻¹ on a motor-driven treadmill. Video records and a geometrical model of the cat hindlimb were used for calculating the rates of change in lengths of the SO, GA and PL muscles. The instantaneous maximum possible force that can be produced by a muscle at a given fibre length and the rate of change in fibre length (termed contractile abilities) were estimated for each muscle throughout the step cycle. Fibre lengths of the SO, GA and PL were calculated using a planar, geometrical muscle model, measured muscle forces and kinematics, and morphological measurements from the animal after it had been killed. Mechanical power and work of SO, GA and PL were calculated for 144 step cycles. The contribution of the positive work done by the ankle extensor muscles of one hindlimb to the increase of the total mechanical energy of the body (estimated from values in the literature) increased from 4–11% at speeds of locomotion of 0.4 and 0.8 ms⁻¹ to 7–16% at speeds of 1.2 ms⁻¹ and

above. The relative contributions of the negative and positive work to the total negative and positive work done by the three ankle extensor muscles increased for GA, decreased for SO and remained about the same for PL, with increasing speeds of locomotion. At speeds of 0.4–0.8 ms⁻¹, the positive work normalized to muscle mass was 7.5–11.0 J kg⁻¹, 1.9–3.0 J kg⁻¹ and 5.3–8.4 J kg⁻¹ for SO, GA and PL, respectively. At speeds of 1.2–1.8 ms⁻¹, the corresponding values were 9.8–16.7 J kg⁻¹, 6.0–10.7 J kg⁻¹ and 13.4–25.0 J kg⁻¹. Peak forces of GA and PL increased and peak forces of SO did not change substantially with increasing speeds of locomotion. The time of decrease of force and the time of decrease of power after peak values had been achieved were much shorter for SO than the corresponding times for GA and PL at fast speeds of locomotion. The faster decrease in the force and power of SO compared with GA and PL was caused by the fast decrease of the contractile abilities and the activation of SO. The results of this study suggest that the ankle extensor muscles play a significant role in the generation of mechanical energy for locomotion.

Key words: muscle power, work output, muscle redundancy, walking, trotting, cat.

Introduction

The SO, GA and PL muscles produce an extension moment at the ankle. This muscle redundancy gives an animal an infinite number of choices of possible force patterns to produce a given joint moment. Measurements of the forces of the SO, GA and PL muscles in the cat show that patterns of muscle forces are relatively stereotypical for a given movement (Abraham and Loeb, 1985; Gregor *et al.* 1988; Herzog and Leonard, 1991; Herzog *et al.* 1993a,b; Walmsley *et al.* 1978). It is not clear why the observed patterns are preferred over

other possible patterns. It may be assumed that animals choose patterns of muscle forces that are advantageous. Presuming that locomotion is a significant factor for animal survival, and considering that locomotion is provided by muscles generating mechanical energy, it may be assumed that the design of the ankle extensor muscles, SO, GA and PL, and the observed activity and force patterns of these muscles during locomotion are well suited for producing mechanical energy. Analysis of the mechanical work done by individual muscles during

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locomotion may aid our understanding of the functional role of the cat ankle extensor muscles.

Power output from muscles is typically studied *in vitro* using the work loop technique (James *et al.* 1995; Josephson, 1985, 1993). This technique allows for simulating muscle behaviour *in vivo* by reproducing the length changes and activation patterns observed during everyday activities. However, little is known about muscle power output *in vivo* and the factors that may be responsible for the differences in the amount of generated mechanical energy between synergistic muscles. In two studies (Biewener *et al.* 1992; Marsh *et al.* 1992), power output was determined *in vivo* from one muscle during animal locomotion. Since, in the cat, SO, GA and PL can produce an extension moment at the ankle, and these muscles have different abilities to produce power (because of differences in their design), the interaction of SO, GA and PL should be studied *in vivo* during power production to improve our understanding of the role of these muscles.

In this study, power and work of cat SO, GA and PL were determined at different speeds of locomotion, and the possible functional roles of these muscles were studied.

Materials and methods

The animal preparation, force and EMG measurements, video filming, and kinematic analysis were as described previously (Allinger and Herzog, 1992; Herzog and Leonard, 1991; Herzog *et al.* 1993a,b). Therefore, only a brief description of the above methods is provided here. Some of the results of muscle force and electromyogram (EMG) measurements from SO and GA of the cats investigated in this study have been reported before (Prilutsky *et al.* 1994a).

Muscle force, EMG recordings and kinematic measurements

Forces and EMG recordings of SO, GA and PL muscles were measured in three outbred, male, adult cats during walking (at speeds of 0.4, 0.8 and 1.2 m s⁻¹) and trotting (at speeds of 1.5 and 1.8 m s⁻¹) on a motor-driven treadmill. 'E'-shaped, stainless-steel tendon force transducers were used for the force measurements. The transducers were surgically implanted onto the separated tendons of the SO, GA and PL muscles under strictly sterile conditions with the animals deeply anaesthetized. To record EMGs from SO, GA and PL, bipolar, indwelling wire electrodes were implanted in the mid-belly of SO, GA and PL approximately parallel to the muscle fibres. Leads of the force transducers and EMG electrodes were drawn subcutaneously to a backpack connector. From this connector, the signals were transmitted by cable or telemetry to a computer (PC386). Before the implantation, the animals were trained to walk and trot on a treadmill at constant speeds up to 2.0 m s⁻¹. For each of the above speeds, force and EMG recordings were obtained for 10–25 step cycles. Muscle forces were recorded at 625 Hz and EMGs at 2500 Hz.

Raw EMG signals were rectified and integrated over 50 ms periods for all step cycles available for a given speed of locomotion. The integration was performed in such a way that

there was a time lag of 50 ms between the integrated EMG (IEMG) and the raw EMG. Discrete IEMG values were connected using an interpolation cubic spline, from which IEMG values were determined for each 1% of every step cycle. Then, these values were normalized with respect to the IEMG peak in a given step cycle and averaged for the three cats and over all step cycles available for a given speed of locomotion.

Simultaneously with muscle force and EMG records, video records of cat locomotion were obtained using a camera (60 Hz, Motion Analysis) with its optical axis aligned perpendicularly to the plane of progression. Force and video records were synchronized using a series of pulses that appeared as spikes on the computer records and as light-emitting diode flashes on the video. Coordinates of reflective skin markers placed over the hip, knee, ankle and metatarsophalangeal joints were obtained from the video records to calculate ankle and knee joint angles.

To reduce measurement errors caused by skin movements with respect to the bones, the position of the knee marker was corrected using information about the length of the tibia and femur, obtained after the cat had been killed. Muscle–tendon lengths of the SO, GA and PL were defined as distances along a straight line from the muscle origin to the tendon insertion. These distances were calculated from the joint angles and morphological measurements of the animals after they had been killed (similar to Goslow *et al.* 1973). The following morphological characteristics were measured in order to calculate the muscle–tendon complex lengths: the length of the tibia, the length from the ankle joint to the tendon insertion of SO, GA and PL, the length along the tibia from the ankle joint to the centroid of origin of SO, the length along the femur from the knee joint to the centroid of origin of GA and PL, and the length of the femur.

Muscle morphological measurements and estimation of muscle contractile abilities

Fibre length and angle of pinnation of the SO, GA and PL were calculated throughout the step cycle using a planar, geometric muscle model (Allinger and Herzog, 1992). The muscle model allowed for tendon elongation using the measured tendon forces of SO, GA and PL during locomotion and the stress–strain properties of tendon (Pollock, 1991). The muscle model also allowed for changes in fibre length and angle of pinnation by assuming that muscle width remained constant during contraction. Fibre lengths and angles of pinnation for SO, GA and PL were assumed to be those of Sacks and Roy (1982) when the muscles were at rest and the ankle and knee joint angles were 90°.

The instantaneous maximal force the muscle could produce (contractile ability) was determined from the instantaneous fibre length and the rate of fibre length change throughout the step cycle as follows:

$$F_{\max}(l,v) = F_v(v) \times F_l(l), \quad (1)$$

where $F_{\max}(l,v)$ is the maximum possible muscle force for a

given fibre length and rate of change in fibre length, $F_v(v)$ is the normalized force as a function of rate of change in fibre length (Spector *et al.* 1980), and $F_l(l)$ is the isometric force as a function of fibre length (Herzog *et al.* 1992).

The isometric force–fibre length relationship was determined from the isometric force (N cm^{-3}) *versus* ankle angle (knee at 90°) relationship of Herzog *et al.* (1992). The volumes of SO, GA and PL were determined using the measured wet mass of each muscle and assuming a density of 1.0564 g cm^{-3} (Mendez and Keys, 1960). Muscle volume was multiplied by the isometric force of Herzog *et al.* (1992) to obtain units of newtons. The ankle angle used by Herzog *et al.* (1992) was converted to muscle–tendon complex length as described above and then converted to fibre length using the muscle model. The result was an isometric force (N) *versus* fibre length (mm) relationship specific to the muscle. Optimal fibre length was determined from this force–fibre length relationship at maximum force for GA and PL. For SO, the optimal fibre length was assumed to occur at an ankle angle of 100° (Rack and Westbury, 1969). Physiological cross-sectional area (PCSA) of the muscles was calculated as the ratio of the muscle volume to the optimal fibre length. The measured and estimated muscle characteristics are presented in Table 1.

Calculation of muscle power and work

The mechanical power produced by the muscles was

Table 1. Characteristics of studied muscles

Characteristics	Cat 1	Cat 2	Cat 3
Animal mass (kg)	5.6	4.6	5.2
SO mass (g)	6.5	3.8	6.0
PL mass (g)	7.0	8.3	10.2
GA mass (g)	23.5	25.2	32.8
SO muscle–tendon complex length (cm)*	9.3	9.2	9.4
PL muscle–tendon complex length (cm)*	12.9	12.7	12.8
GA muscle–tendon complex length (cm)*	13.0	12.8	12.8
SO tendon to belly length ratio*	1.2	1.2	1.3
GA tendon to belly length ratio*	4.9	4.9	4.9
PL tendon to belly length ratio*	6.0	5.9	5.9
SO optimal fibre length (cm)	3.9	4.0	3.9
PL optimal fibre length (cm)	2.1	1.9	2.2
GA optimal fibre length (cm)	2.4	2.3	2.5
SO pinnation angle (degrees)*	7	7	7
PL pinnation angle (degrees)*	14	14	14
GA pinnation angle (degrees)*	19	19	19
SO PCSA (cm^2)	1.6	0.9	1.5
PL PCSA (cm^2)	3.2	4.0	4.4
GA PCSA (cm^2)	9.3	10.4	12.4
SO F_{\max} (N)	43.7	25.5	39.8
PL F_{\max} (N)	62.4	74.2	92.2
GA F_{\max} (N)	205.2	220.2	287.6

*Determined for an ankle and knee angle of 90° .

SO, soleus muscle; PL, plantaris muscle; GA, gastrocnemius muscle; PCSA, physiological cross-sectional area; F_{\max} , maximum muscle force for a given fibre length and rate of change of fibre length.

calculated as the scalar product of the muscles' force and the relative velocity of the attachment points. By definition, concentric contractions give positive power and eccentric contractions give negative power. The rate of change in length of the muscles was computed after smoothing the muscle length–time data (Butterworth low-pass filter, 12.5 Hz cut-off frequency) using a finite difference method (Winter, 1979). The cut-off frequency was found using a Fourier analysis of the muscle length as a function of time. The muscle powers were calculated at each 1% of each step cycle using an interpolation cubic spline. Negative and positive mechanical work done by a muscle for a given step cycle was calculated as:

$$-W^m = \sum_{i=2}^N \frac{\Delta t}{2} (P_i^m + P_{i-1}^m), \text{ if } (P_i^m + P_{i-1}^m) < 0, \quad (2)$$

$$+W^m = \sum_{i=2}^N \frac{\Delta t}{2} (P_i^m + P_{i-1}^m), \text{ if } (P_i^m + P_{i-1}^m) > 0, \quad (3)$$

where $-W^m$ and $+W^m$ are the negative and positive mechanical work done by a muscle, respectively; P_i^m and P_{i-1}^m are the muscle powers at the i th and $(i-1)$ th film frames, respectively; N is the number of frames of a given step cycle; and Δt is the time between video frames.

The total mechanical power (P_i^{tot}) of the three muscles, SO, GA and PL, at the i th film frame was equal to the sum of the powers of the individual muscles. The total negative and positive mechanical work of the three muscles was calculated as:

$$-W^{\text{tot}} = \sum_{i=2}^N \frac{\Delta t}{2} (P_i^{\text{tot}} + P_{i-1}^{\text{tot}}), \text{ if } (P_i^{\text{tot}} + P_{i-1}^{\text{tot}}) < 0, \quad (4)$$

$$+W^{\text{tot}} = \sum_{i=2}^N \frac{\Delta t}{2} (P_i^{\text{tot}} + P_{i-1}^{\text{tot}}), \text{ if } (P_i^{\text{tot}} + P_{i-1}^{\text{tot}}) > 0, \quad (5)$$

where $-W^{\text{tot}}$ and $+W^{\text{tot}}$ are the total negative and total positive mechanical work done by the three muscles, respectively; P_i^{tot} and P_{i-1}^{tot} are the total power of the three muscles at the i th and $(i-1)$ th film frames, respectively; N is the number of frames of a given step cycle; and Δt is the time between video frames. The relative contribution of the individual ankle extensor muscles (RC^m) to the total negative and positive mechanical work was calculated as follows:

$$-RC^m = [-W^m / -W^{\text{tot}}] \times 100\%, \quad (6)$$

$$+RC^m = [+W^m / +W^{\text{tot}}] \times 100\%. \quad (7)$$

In addition, plots of muscle force *versus* muscle–tendon complex length and muscle force *versus* fibre length (work loops; Josephson, 1985) were constructed.

In order to compare results across cats and muscles, muscle forces were normalized to PCSA, muscle–tendon complex lengths were normalized to the muscle–tendon complex length at an ankle and knee angle of 90° , fibre lengths were normalized to the optimal fibre length, and muscle power and

work were normalized to the muscle mass. A total of 144 step cycles was analyzed.

Results

Total mechanical power and work of the three ankle extensor muscles

The mean (\pm S.D.) total mechanical power of SO, GA and PL as a function of normalized step cycle time is shown in Fig. 1 for three cats and different speeds of locomotion. At the beginning of the support phase (approximately the first one-eighth to the first one-third of the support phase, depending on the speed of locomotion), total power was negative. Total power then became positive for the remainder of the support phase. For approximately the first half of the swing phase, total

power was negative; it became positive for the remainder of the swing phase. When the speed of locomotion increased, the phase of negative power during the support phase tended to be longer relative to the corresponding phase of positive power. In absolute terms, the length of the negative power phase decreased on average from 0.107 to 0.047 s when the speed of locomotion increased from 0.4 to 1.8 m s⁻¹. The corresponding times for the phase of positive power were 0.418 and 0.110 s, respectively.

The peak magnitude of the total power was higher during the support phase than during the swing phase. The peak negative power tended to increase as speeds increased (Fig. 1). The peak positive power increased 5–10 times from the lowest to the highest speed of locomotion measured for the different animals.

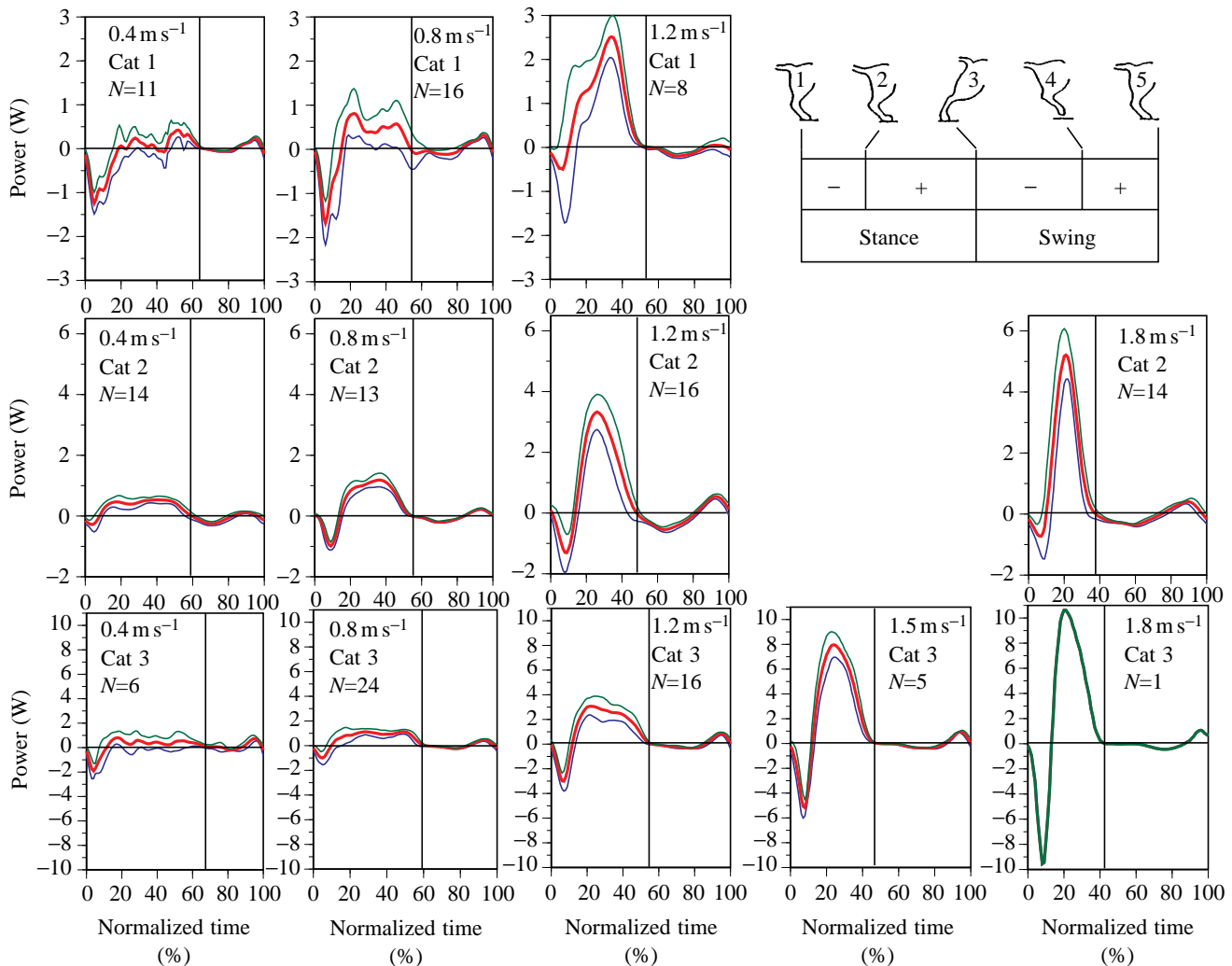


Fig. 1. Mean (thick line) and standard deviation (thin lines) of the total mechanical power of the soleus (SO), gastrocnemius (GA) and plantaris (PL) muscles as a function of normalized step cycle time. The data are presented for three cats and different speeds of locomotion; N is the number of step cycles analyzed. Touch-down occurs at time 0%. The vertical lines separate the support and swing phases. Cat hindlimb positions at different instances of the step cycle are shown in the top right-hand corner. Positions 1 and 5 correspond to paw contact (the beginning of the step cycle), position 2 corresponds to the beginning of extension at the ankle during the stance phase, position 3 corresponds to the end of the stance phase, position 4 corresponds to the beginning of extension at the ankle joint during the swing phase. – and + show the phases of negative and positive power, respectively.

The mean (\pm S.D.) total negative and positive mechanical work per step cycle are presented in Table 2 for all animals and speeds. The absolute values of the total positive work were 1.5–5 times higher than those of the negative work (except cat 1, speed 0.4 m s^{-1} , Table 2); that is, the total net work done by the muscles ($-W^{\text{tot}} + W^{\text{tot}}$) was typically positive. These differences increased with increasing speeds of locomotion. There was no systematic change of the total negative work with increasing speeds of locomotion. The total positive work increased 2–5 times for the different animals when speed increased from 0.4 to 1.2 m s^{-1} (cats 1 and 2) or 1.5 m s^{-1} (cat 3). When speed increased from 1.2 to 1.8 m s^{-1} (cat 2), or from 1.5 to 1.8 m s^{-1} (cat 3), the total positive work decreased slightly (Table 2).

Mechanical power and work of individual ankle extensor muscles

Mean absolute power, force and velocity of SO, GA and PL as functions of the normalized step cycle time are shown in Fig. 2 for cat 3. All muscles underwent a stretch–shorten cycle in the support and the swing phases. There were no substantial differences between SO, GA and PL in the length of the stretch and the shorten phases. SO tended to have the highest peak velocities of elongation and shortening, while PL had the lowest. When the speed of locomotion increased, peak muscle velocities tended to increase as well. Peak velocities during the stretch phase of the support period increased from 0.01 to 0.03 m s^{-1} for cat 2, and from 0.03 to 0.08 – 0.12 m s^{-1} for cat 3 (Fig. 2). Corresponding peak velocities of the three muscles of cat 1 did not increase with increasing speeds of locomotion.

Table 2. Mean total mechanical work of SO, GA and PL per step cycle

Speed (m s^{-1})	Duration of cycle (ms)	Number of studied cycles	$-W^{\text{tot}}$ (mJ)	$+W^{\text{tot}}$ (mJ)	$-W^{\text{tot}} + W^{\text{tot}}$ (mJ)
Cat 1					
0.4	712 \pm 47	11	-106 \pm 18	74 \pm 26	-32 \pm 31
0.8	602 \pm 36	16	-91 \pm 37	139 \pm 28	48 \pm 43
1.2	458 \pm 10	8	-45 \pm 18	261 \pm 88	216 \pm 101
Cat 2					
0.4	749 \pm 73	14	-44 \pm 10	165 \pm 27	121 \pm 23
0.8	572 \pm 25	13	-58 \pm 7	196 \pm 19	138 \pm 18
1.2	396 \pm 25	16	-83 \pm 15	339 \pm 95	256 \pm 50
1.8	376 \pm 12	14	-51 \pm 13	290 \pm 37	239 \pm 43
Cat 3					
0.4	833 \pm 119	6	-77 \pm 34	143 \pm 79	66 \pm 93
0.8	620 \pm 45	24	-63 \pm 14	294 \pm 56	231 \pm 62
1.2	513 \pm 42	16	-124 \pm 28	472 \pm 50	348 \pm 57
1.5	420 \pm 23	5	-165 \pm 29	705 \pm 49	540 \pm 68
1.8	400	1	-264	696	432

Values are means \pm S.D.

$-W^{\text{tot}}$ is the total negative work.

$+W^{\text{tot}}$ is the total positive work.

For other abbreviations see Table 1.

The peak velocity of shortening during the support phase increased substantially (from 0.02 – 0.05 to 0.1 – 0.18 m s^{-1}) for all animals as speed increased.

Force–time histories were consistent for the three cats. Forces in all muscles increased from the beginning of the support phase, reached a peak, and decreased to a value close to zero at the end of the support phase. Forces were small during the swing phase and tended to increase just before touch-down of the next step cycle. Peak forces of GA were typically reached before those of SO, except for animal 3 at speeds of 1.5 and 1.8 m s^{-1} . Peak PL forces were always reached later than peak SO and GA forces for all animals and all speeds. The peak forces of GA and PL increased 2–3 times, whereas the peak forces of SO did not change substantially with increasing speeds of locomotion (Fig. 2). During approximately the first two-thirds of the support period, the forces of GA were higher than those of SO and PL at all speeds of locomotion. Typically, the forces of PL were similar to those of GA during the last third of the support period. At speeds of 0.4 and 0.8 m s^{-1} , SO forces were typically higher than those of GA during the last third of the support period. At a speed of 0.4 m s^{-1} , the times from maximum to minimum force of SO, GA and PL during the support period were almost the same. With increasing speeds of locomotion, minimum forces were reached sooner after maximum forces for SO than for GA and PL during the support phase (Fig. 2).

The phases in which individual muscle powers of SO, GA and PL were negative and positive agreed well with those described for the total power. Peak negative and peak positive power of SO, GA and PL typically increased with increasing speeds of locomotion. The peak negative power of GA during the support and the swing phases was greater in magnitude than the corresponding values for SO and PL for all cats and all speeds of locomotion. The peak negative power of PL tended to be less than those of SO and GA (Fig. 2). At speeds of 0.4 and 0.8 m s^{-1} , differences among absolute positive powers of SO, GA and PL were typically minimal during the support phase. When the speed of locomotion increased from 0.8 to 1.5 – 1.8 m s^{-1} , differences in positive power of SO, GA and PL during the support period increased. GA had the highest values during approximately the first three-quarters of the period of positive power during the support phase, whereas SO had the lowest values of positive power during the whole phase of positive power at these speeds of locomotion. During approximately the last quarter of this phase, GA and PL powers were similar (Fig. 2).

Normalized powers of SO, GA and PL averaged across cats and step cycles are shown in Fig. 3. The decrease in the peak normalized power from 1.5 to 1.8 m s^{-1} was primarily caused by the results from cat 2 (14 out of the 15 analyzed step cycles) which had substantially lower absolute and normalized powers, forces and velocities of SO, GA and PL at 1.8 m s^{-1} compared with 1.5 m s^{-1} . The peak power normalized to muscle mass was high for SO and PL (up to 230 – 280 W kg^{-1} at a speed of 1.5 m s^{-1} , Fig. 3) and low for GA (approximately 110 W kg^{-1} , Fig. 3).

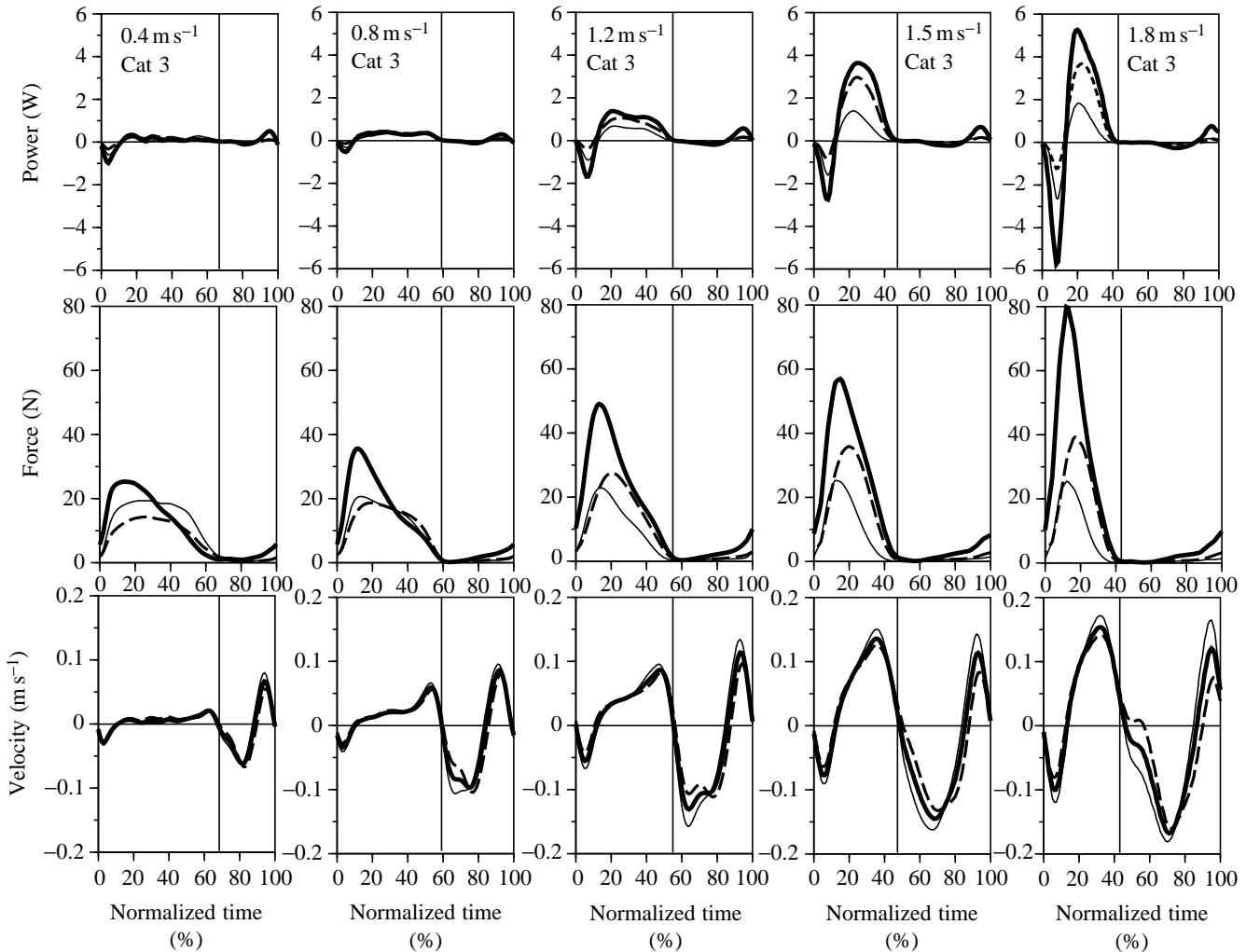


Fig. 2. Averaged power, force and velocity of individual ankle extensor muscles (SO, GA and PL) as functions of normalized step cycle time. The data presented are for cat 3. The solid, thin lines represent SO; the solid, thick lines represent GA; the dashed lines represent PL. Touch-down occurs at time 0%. The vertical lines separate the support and swing phases.

The relationships between the normalized forces and the normalized muscle–tendon complex lengths (work loops) of SO, GA and PL are shown in Fig. 4 for different speeds of locomotion. The peak SO forces normalized to PCSA were the highest among the three muscles (115–165 kN m^{-2} , Fig. 4). The peak normalized GA forces increased from approximately 20 kN m^{-2} (0.4 m s^{-1}) to 43 kN m^{-2} (1.5 m s^{-1}); the corresponding values of the normalized force for PL were 32 and 77 kN m^{-2} , respectively. The area inside the work loop represents the net work done by the muscle. With increasing speeds of locomotion, the net work increased for all three muscles because of the corresponding increases in muscle force and/or muscle length change. During the early phase of support, muscles elongated by approximately 2–6% of their length (or about 2.5–5.6 mm for SO and 1.3–4.0 mm for GA and PL). After this elongation, muscles shortened by approximately 5–16% (4.7–15 mm for SO and 3.5–14 mm for GA and PL). The magnitude of muscle shortening during the stance phase typically increased with increasing speeds of

locomotion (Fig. 4). The length at which peak forces occurred shifted to longer muscle lengths as speed increased.

The shapes of the muscle force–fibre length loops (Fig. 5) were slightly different from those of the force–muscle–tendon complex loops (Fig. 4). Muscle fibres of SO elongated little, and fibres of GA and PL remained virtually isometric during the early phase of support. With increasing speeds, the fibre length at touch-down increased from $0.92L_0$ to $1.2L_0$ for SO, from $0.8L_0$ to $1.05L_0$ for GA and from $0.72L_0$ to $1.1L_0$ for PL, where L_0 is the optimal fibre length. The length at which peak forces occurred also increased with increasing speeds of locomotion (Fig. 5).

Typically, the positive work done by all muscles was higher than the negative work (Table 3). The difference between positive and negative work tended to increase with increasing speeds of locomotion (Table 3; Figs 4, 5). Absolute values of positive work of SO, GA and PL did not change substantially for speeds of locomotion of 1.2 m s^{-1} and above. Absolute values for the negative work of PL were typically smaller than

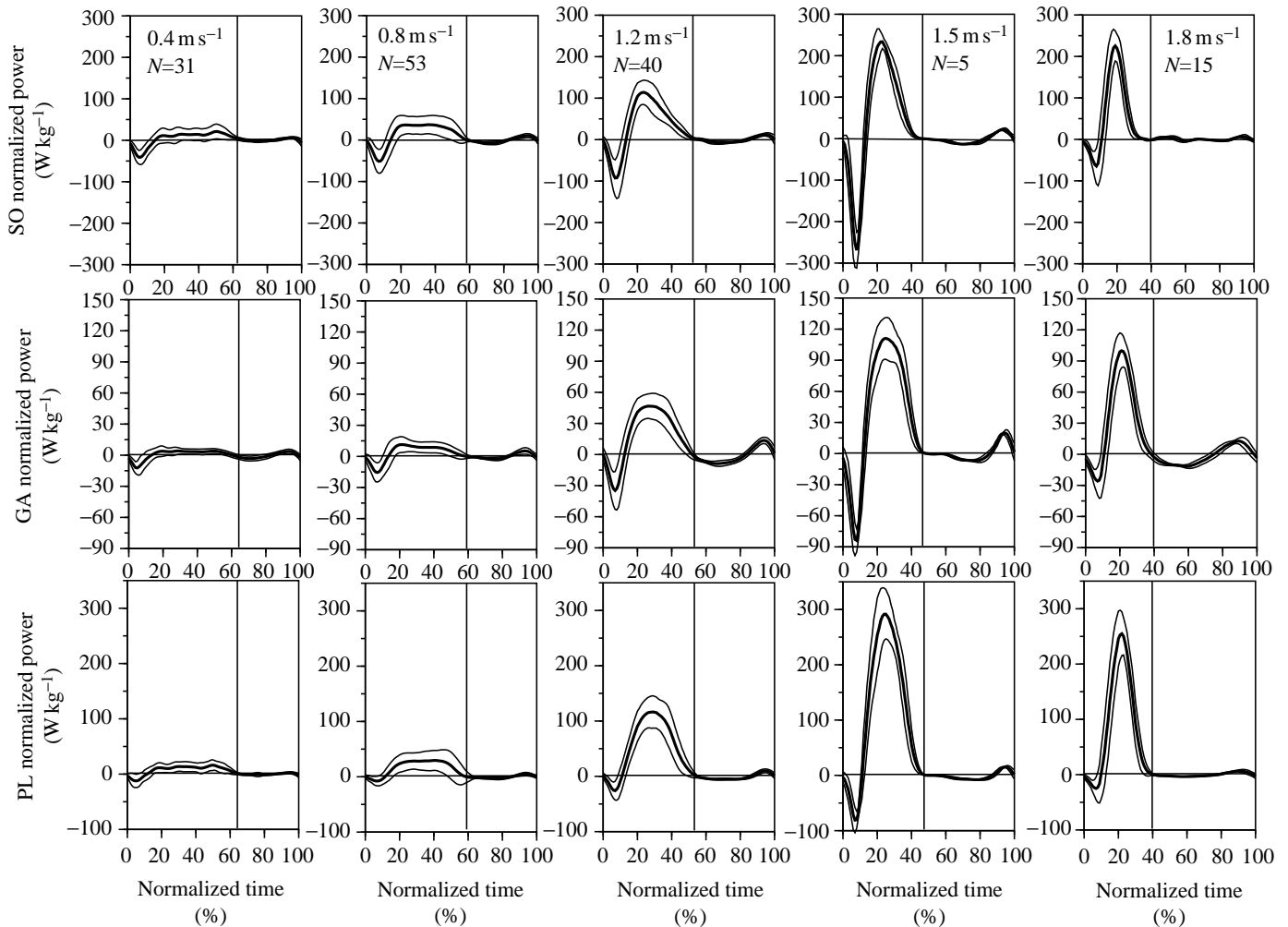


Fig. 3. Mean (thick line) and standard deviation (thin lines) of normalized power of SO, GA and PL as functions of normalized step cycle time. The power was normalized with respect to muscle mass. The data were averaged over the three cats and all step cycles available for each speed of locomotion. N is the number of step cycles analyzed. Touch-down occurs at time 0%. The vertical lines separate the support and swing phases.

those for SO and GA at all speeds of locomotion. At speeds of 0.4 and 0.8 m s^{-1} , the values of the absolute positive work of SO, GA and PL were similar. When speed increased, the differences in the absolute positive work done by SO, GA and PL increased. GA had the highest values for the positive work at speeds greater than 0.8 m s^{-1} ; SO had the lowest (Table 3).

The average values and standard deviations of the negative and positive mechanical work of SO, GA and PL per step cycle normalized to muscle mass are presented in Table 4. Values of the normalized positive work done by SO were the highest among the three muscles at speeds of 0.4 and 0.8 m s^{-1} (7.5 – 11.0 J kg^{-1}). At these speeds, the normalized positive work of PL was slightly lower (5.3 – 8.4 J kg^{-1}), and the work of GA was the lowest among the three muscles (1.9 – 3.0 J kg^{-1}). With increasing speeds of locomotion above 0.8 m s^{-1} , the normalized positive work done by PL became higher than that of SO (13.4 – 25.0 J kg^{-1} versus 9.8 – 16.7 J kg^{-1} ; the corresponding values of GA work were 6.0 – 10.7 J kg^{-1}).

Relative contributions of SO, GA and PL to the absolute total negative and positive work are illustrated in Fig. 6. The contributions of SO to the total negative and positive work tended to decrease and the corresponding contributions of GA tended to increase with increasing speeds of locomotion. The contributions of the negative and positive work of PL to the total negative and positive work remained nearly constant with increasing speeds of locomotion.

Contractile abilities and activity of SO, GA and PL

The contractile abilities of the three muscles were not constant during the step cycle: they were higher when the muscles contracted isometrically or elongated and were lower when the muscles shortened (Fig. 7). At about 5–7% of the normalized cycle time, the contractile abilities were close to 100% of the maximum isometric forces and then the contractile abilities started to decrease, reaching a minimum at the end of the stance phase. The minimum values of the contractile abilities in the stance phase decreased from

Table 3. Mean mechanical work of SO, GA, and PL per step cycle

Speed (m s ⁻¹)	Number of studied cycles	-W ^{SO} (mJ)	+W ^{SO} (mJ)	-W ^{GA} (mJ)	+W ^{GA} (mJ)	-W ^{PL} (mJ)	+W ^{PL} (mJ)
Cat 1							
0.4	11	-52±7	28±10	-43±15	20±8	-13±9	28±9
0.8	16	-41±13	44±6	-42±16	54±14	-11±12	43±10
1.2	8	-17±8	61±32	-25±12	114±36	-7±1	89±21
Cat 2							
0.4	14	-5±2	38±7	-33±6	72±13	-6±2	55±9
0.8	13	-14±1	39±2	-32±4	83±10	-12±2	75±8
1.2	16	-8±3	39±11	-65±9	183±52	-11±3	118±32
1.8	14	-5±3	36±6	-41±8	147±20	-7±3	109±14
Cat 3							
0.4	6	-33±18	45±27	-35±14	53±30	-12±5	48±23
0.8	24	-20±4	86±13	-33±7	111±29	-11±2	99±17
1.2	16	-38±10	95±10	-70±15	221±28	-19±4	157±18
1.5	5	-49±9	100±3	-91±15	352±32	-26±6	255±20
1.8	1	-67	97	-163	354	-35	245

Values are means ± s.d.

-W^{SO}, -W^{GA} and -W^{PL} are the negative work of SO, GA and PL, respectively.

+W^{SO}, +W^{GA} and +W^{PL} are the positive work of SO, GA and PL, respectively.

For other abbreviations see Table 1.

40–55 % at 0.4 m s⁻¹ to 6–20 % at 1.8 m s⁻¹. The contractile abilities of SO during the late support phase were the lowest among the three muscles at speeds of 0.8 m s⁻¹ and above, and the difference in the contractile abilities between SO and GA and PL increased with increasing speeds of locomotion.

The normalized IEMG of SO, GA and PL started to increase at 75–85 % of the normalized step cycle time depending on the speed of locomotion (Fig. 7). IEMG reached its maximum at about 5–13 % of the normalized step cycle time and then started to decrease, reaching values close to zero towards the end of the stance phase. The IEMG of SO reached its minimum increasingly faster compared with those of GA and PL as speed of locomotion increased. During the last third of the stance phase at speeds of 1.5 and 1.8 m s⁻¹, the magnitude of the normalized IEMG of SO was up to 40 % lower than those of GA and PL (Fig. 7).

Discussion

Some of the results obtained in this study can be compared with corresponding data reported in the literature. The patterns and magnitudes of the absolute velocity of SO and GA are similar to those reported by Gregor *et al.* (1988) for SO, and by Goslow *et al.* (1973) for SO and the medial gastrocnemius. According to our results (Fig. 2) and the data of Goslow *et al.* (1973, their Table 5), peak velocities of SO were always higher than those of GA. This finding can be explained by the two-joint nature of the GA muscle. During locomotion, shortening (or elongation) of GA, associated with the action of the ankle joint, is usually offset partly by a corresponding elongation (or

Table 4. Mean mechanical work of SO, GA and PL per step cycle normalized to muscle mass

Speed (m s ⁻¹)	Number of studied cycles	-W (J kg ⁻¹)	+W (J kg ⁻¹)	-W + +W (J kg ⁻¹)
Soleus				
0.4	31	-4.5±3.4	7.5±3.5	3.0±6.4
0.8	53	-4.4±1.7	11.0±3.6	6.6±4.9
1.2	40	-4.0±2.3	11.5±4.4	7.6±3.7
1.5	5	-8.2±1.4	16.7±0.5	8.5±1.1
1.8	15	-1.9±2.6	9.8±2.3	7.9±1.8
Gastrocnemius				
0.4	31	-1.4±0.5	1.9±1.1	0.5±1.3
0.8	53	-1.3±0.5	3.0±0.9	1.7±1.1
1.2	40	-2.0±0.7	6.00±1.3	4.0±1.3
1.5	5	-2.8±0.4	10.7±1.0	7.9±1.3
1.8	15	-1.9±0.9	6.2±1.5	4.3±1.0
Plantaris				
0.4	31	-1.2±0.9	5.3±0.9	4.1±2.2
0.8	53	-1.3±1.0	8.4±2.1	7.1±2.5
1.2	40	-1.5±0.5	13.4±2.7	11.9±2.6
1.5	5	-2.6±0.6	25.0±2.0	22.4±2.1
1.8	15	-1.0±0.7	13.9±3.2	12.9±2.8

Values are means ± s.d.

-W is the negative work of the muscle and +W is the positive work of the muscle.

shortening) at the knee joint (Goslow *et al.* 1973). Peak absolute velocities of PL were typically lower than those of GA (Fig. 2) because (a) the moment arms of PL and GA were

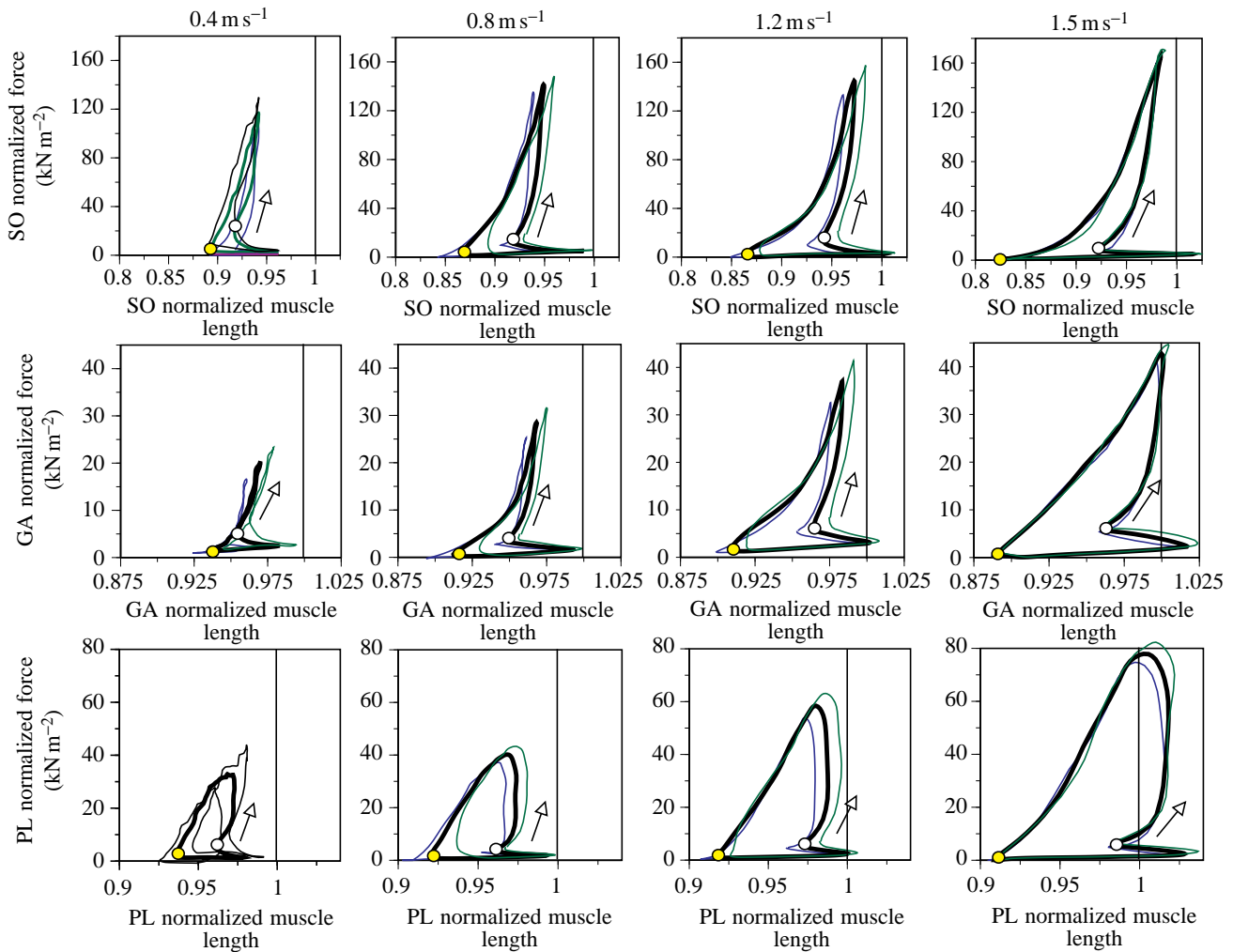


Fig. 4. Normalized muscle forces of SO, GA and PL as functions of the normalized muscle–tendon complex lengths (the work loops) during the step cycle. The thick lines represent mean forces and lengths, the thin lines represent standard deviations of forces and lengths. The data were averaged for the three cats and over all step cycles available for each speed of locomotion. The arrows show the direction of the loop formation. The open circles correspond to the beginning of the stance phase, the shaded circles correspond to the end of the stance phase. Muscle forces were normalized with respect to the muscle physiological cross-sectional area (PCSA), muscle–tendon complex lengths were normalized with respect to the muscle–tendon complex length at an ankle and knee angle of 90° (see Table 1). The vertical lines correspond to the normalized muscle–tendon complex length of 1.

almost the same about the ankle joint, and (b) the moment arm of PL about the knee joint was always larger than that of GA.

Muscle fibres of GA and PL do not necessarily stretch during the early stance phase, while the muscle–tendon complex length increases (Figs 4, 5). The lengths of muscle fibres of the cat medial gastrocnemius obtained using ultrasound techniques were similar to those estimated in this study (see Griffiths, 1991; Hoffer *et al.* 1989). These results suggest that the tendon and/or aponeurosis take up part of the muscle–tendon complex length change and so may contribute to the absorption and recovery of mechanical energy. The tendon contributions to the positive work done by SO, GA and PL in the cat at speeds of 0.4 – 1.8 m s^{-1} were estimated to be 50–14%, respectively (Prilutsky *et al.* 1994c).

The patterns and magnitudes of SO, GA and PL forces recorded in this study are consistent with results reported by

Fowler *et al.* (1993), Gregor *et al.* (1988), Herzog and Leonard (1991), Herzog *et al.* (1993a) and Walmsley *et al.* (1978).

Absolute negative work of the SO and medial gastrocnemius muscles has been reported to decrease with increasing speeds of locomotion (Whiting *et al.* 1984; Gregor *et al.* 1988). This observation was consistent with our results for cat 1. Absolute positive work of SO and GA has been reported to increase with increasing speeds of locomotion (Whiting *et al.* 1984) and also tended to increase in the present study. Changes in power of SO and GA with increasing speeds of locomotion obtained in this study (Fig. 2) were similar to those reported by Whiting *et al.* (1984, their Fig. 6). The peak power of GA was usually higher in the present study than in that by Whiting *et al.* (1984), in which the power in the medial head of the GA was determined. The normalized powers of SO, GA and PL (Fig. 3) were within the range of powers determined *in vivo* for the

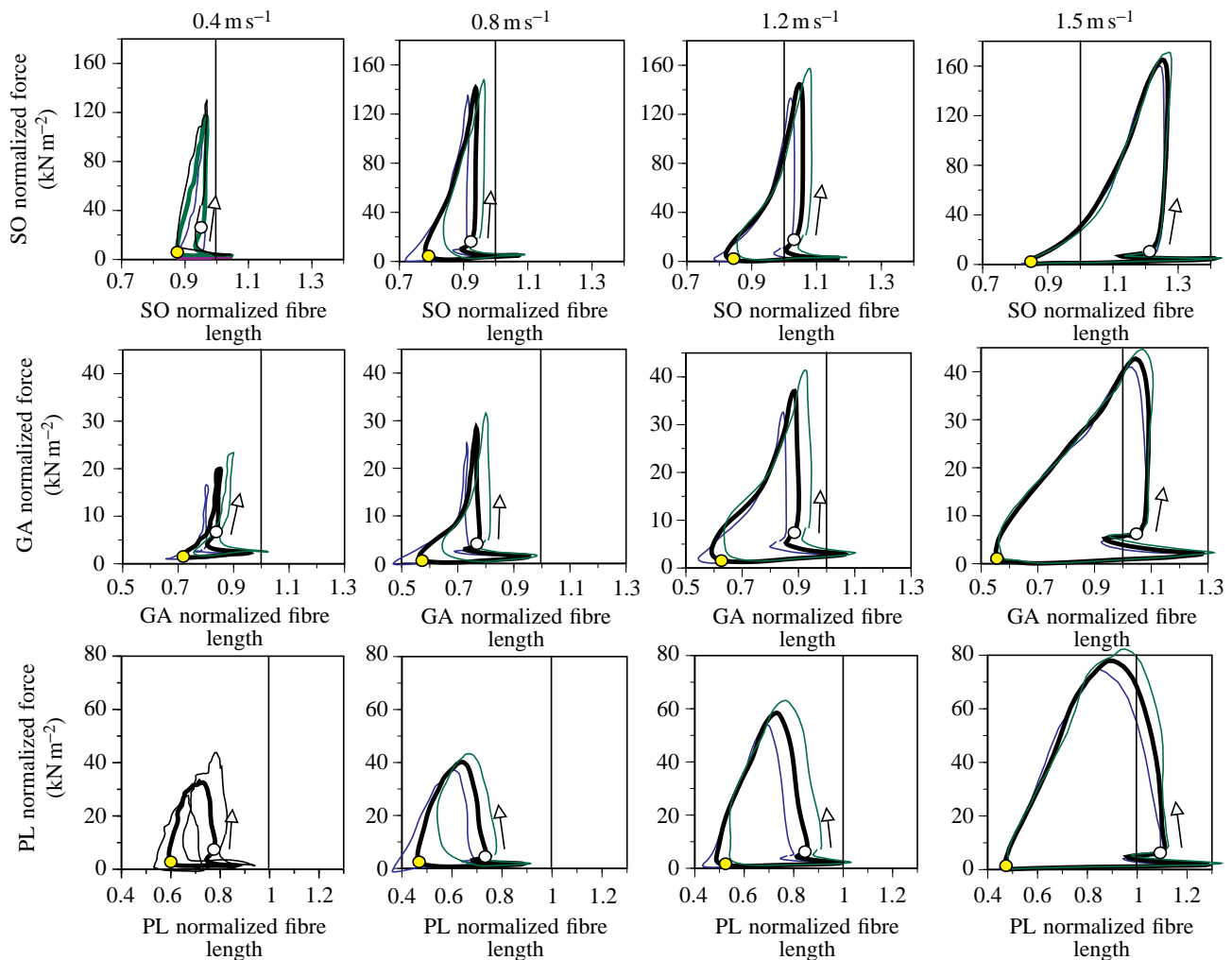


Fig. 5. Normalized muscle forces of SO, GA and PL as functions of the normalized fibre lengths (the work loops) during the step cycle. The thick lines represent mean muscle forces and fibre lengths, the thin lines represent standard deviations of forces and fibre lengths. The data are averaged for the three cats and over all step cycles available for each speed of locomotion. The arrows show the direction of loop formation. The open circles correspond to the beginning of the stance phase, the shaded circles correspond to the end of the stance phase. Muscle forces were normalized with respect to the muscle physiological cross-sectional area (PCSA), fibre lengths were normalized with respect to the optimal fibre length (see Table 1). The vertical lines correspond to the optimal fibre length.

pectoralis muscle during flight in the starling (Biewener *et al.* 1992) and for the adductor muscle in the scallop during jet-propulsion swimming (Marsh *et al.* 1992).

Ankle extensor muscles as generators of mechanical energy

According to measurements of the physiological cross-sectional areas (Sacks and Roy, 1982) and the maximal moments of muscles crossing the ankle joint (Lawrence *et al.* 1993), GA, SO and PL are the main ankle extensor muscles. However, their role in generating mechanical energy during locomotion has not been estimated. An estimate of the contribution of the ankle extensor muscles to the increase in the total mechanical energy for one step cycle of the cat may be made by using the equation reported by Heglund *et al.* (1982). Using this equation, the 'total' positive work, $+\Delta E^{\text{tot}}$, required for walking and trotting for each cat was calculated for speeds of 0.4–1.8 m s^{-1} and was compared with the corresponding

values of the total positive work of SO, GA and PL ($+W^{\text{tot}}$) (Table 5). Values of $+\Delta E^{\text{tot}}$ increased from 1578 to 5158 mJ as the speed of locomotion increased from 0.4 to 1.8 m s^{-1} . The corresponding increase of $+W^{\text{tot}}$ was from 74–165 mJ at a speed of 0.4 m s^{-1} to 290–696 mJ at a speed of 1.8 m s^{-1} (Tables 2, 5). Therefore, the estimated relative contribution of work of SO, GA and PL of one hindlimb to $+\Delta E^{\text{tot}}$ increased from 4–11% at a speed of 0.4 m s^{-1} to 7–16% at speeds of 1.2–1.8 m s^{-1} . From these results, it appears that SO, GA and PL play a significant role in generating mechanical energy during locomotion. This role becomes more important with increasing speeds of locomotion up to 1.2 m s^{-1} .

Features of power and force patterns of individual ankle extensor muscles

SO, GA and PL have a different architecture, different morphological, contractile and mechanical properties, and

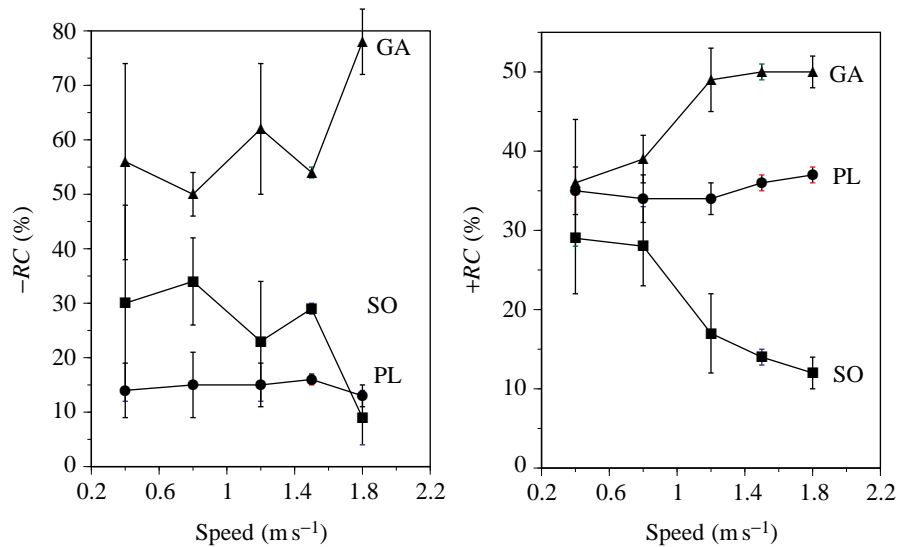


Fig. 6. Relative contribution (mean and standard deviation) of the negative ($-RC$) and positive ($+RC$) work of individual ankle extensor muscles (SO, GA and PL) to the total negative and positive work of these muscles as a function of the speed of locomotion.

Table 5. Mean contribution of the total positive work of SO, GA and PL of one hindlimb to an increase of total mechanical energy of a body during a cycle of locomotion

Speed (m s ⁻¹)	$+W^{\text{tot}}$ (mJ)	$+\Delta E^{\text{tot}}$ (mJ)	$+W^{\text{tot}}/+\Delta E^{\text{tot}} \times 100$ (%)
0.4	74–165	1578–2049	4–11
0.8	139–294	2516–3225	4–10
1.2	261–472	2808–4126	7–12
1.5	705	4343	16
1.8	290–696	4335–5158	7–14

$+W^{\text{tot}}$ is the total positive work of SO, GA and PL.

$+\Delta E^{\text{tot}}$ is an increase of the total mechanical energy of a body, calculated using the equation from Heglund *et al.* (1982) for different speeds of locomotion and the three cats studied.

For other abbreviations see Table 1.

different attachments (Table 1). SO is primarily composed of slow, low-threshold, fatigue-resistant motor units (Burke *et al.* 1974) and has relatively long muscle fibres (Sacks and Roy, 1982), a relatively short tendon (Walmsley and Proske, 1981) and a low maximum isometric force and maximum shortening velocity (Spector *et al.* 1980). SO is a one-joint muscle. GA has many of the opposite properties of SO. GA is primarily composed of fast, high-threshold, fatiguable motor units (Burke *et al.* 1973). It has short muscle fibres (Sacks and Roy, 1982), a longer tendon than SO (Walmsley and Proske, 1981) and a high maximum isometric force and maximum velocity of shortening (Spector *et al.* 1980). GA is a two-joint muscle. PL has properties that appear to be intermediate between those of SO and GA (Table 1). PL has about the same percentage of fast motor units as GA (Baldwin *et al.* 1984; West *et al.* 1986). Its physiological cross-sectional area, mass and the maximum isometric force are larger than those of SO and smaller than those of GA (Herzog *et al.* 1992; Sacks and Roy, 1982). PL spans the knee and ankle. Also, PL is partly attached to the

tendon of the flexor digitorum brevis and, therefore, can cause flexion in the metatarsophalangeal joints.

At slow speeds of locomotion (0.4 and 0.8 m s⁻¹), the slow, low-threshold SO produced approximately the same values of positive power (Fig. 2) and did a similar amount of positive work (Table 3; Fig. 6) as the fast and strong GA and PL. At these speeds of locomotion, slow, low-threshold motor units of GA and PL were probably recruited (Walmsley *et al.* 1978). The amount of work required to extend the ankle at slow speeds of locomotion could be done by GA and PL exclusively, by recruiting additional motor units with a higher threshold than that of already recruited motor units (Walmsley *et al.* 1978). However, an increase in the percentage of motor units with a higher threshold participating in the generation of mechanical energy might increase metabolic energy expenditure, because motor units with a higher threshold may have a lower mechanical efficiency in doing positive work (Barclay, 1994; Davies, 1965; Gibbs and Gibson, 1972; Wendt and Gibbs, 1973).

As shown in the previous section, an increase in the speed of locomotion appears to be associated with an increase in the power, velocity and work done by SO, GA and PL, and with an increase in the force of GA and PL. SO could provide an increase in force and do more work at speeds of locomotion of 0.8–1.8 m s⁻¹ because this muscle is not fully activated during the late phase of support at these speeds (Fig. 7; see also Figs 4, 5 in Prilutsky *et al.* 1994a). However, the slow maximum velocity of shortening of SO (Spector *et al.* 1980) and the stiff muscle–tendon complex of this muscle [the tendon length to muscle fibre length ratio is approximately 1–2 (Zajac, 1989; Table 1), which makes the difference in shortening velocities between the muscle–tendon complex and fibres smaller (Alexander and Ker, 1990; Zajac, 1989)] cause a faster decrease in the contractile abilities of SO compared with those of GA and PL during the late support period at high speeds of locomotion (Fig. 7). Estimates of the shortening velocity of fibres normalized to the optimal length and maximum shortening velocity (Prilutsky *et al.* 1994a) showed that, with

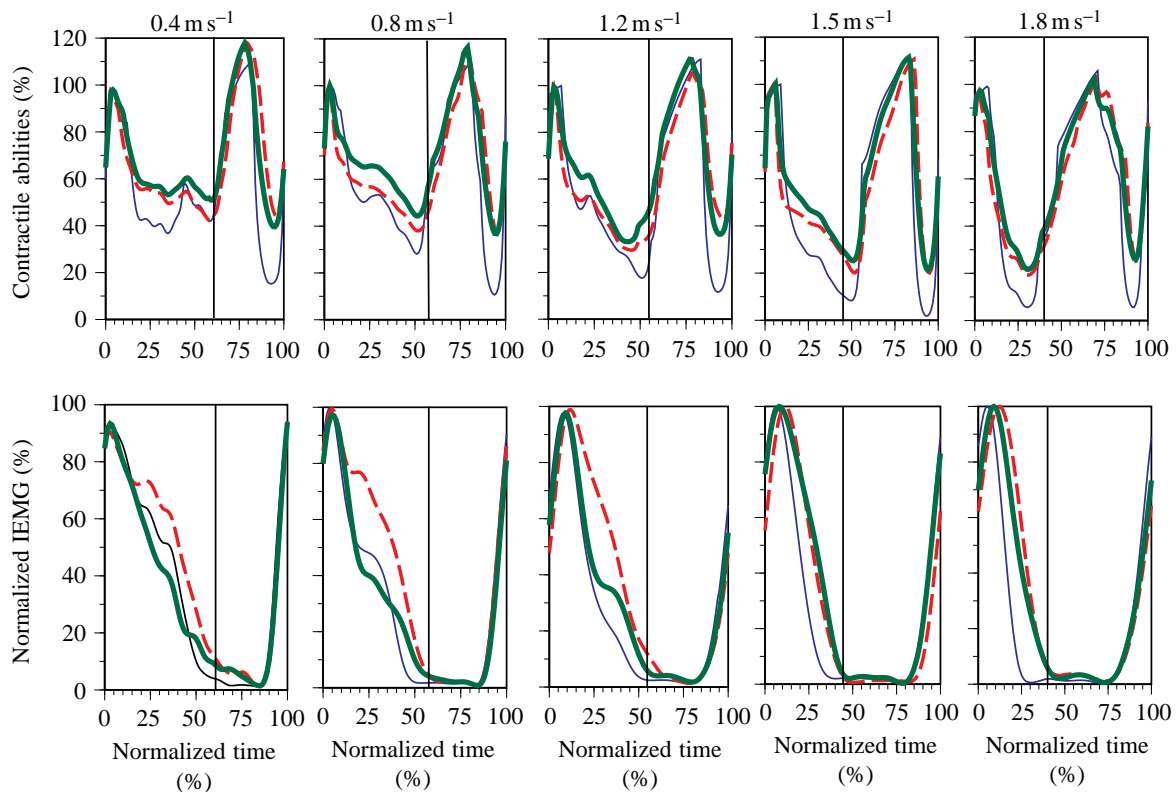


Fig. 7. Averaged normalized contractile abilities and integrated EMG (IEMG) of SO, GA and PL as functions of normalized step cycle time. The contractile abilities (maximum possible force that can be produced at a given fibre length and rate of fibre length change) were normalized with respect to the estimated maximum isometric muscle force (see Table 1). IEMGs were normalized with respect to the peak IEMG in a step cycle. The data were averaged for the three cats and over all step cycles available for each speed of locomotion. The solid, thin lines represent SO; the solid, thick lines represent GA; the dashed lines represent PL. Touch-down occurs at time 0%. The vertical lines separate the support and swing phases.

increasing speeds of locomotion, the normalized velocity of shortening increased faster for fibres of SO than for fibres of GA. Note that GA has a high intrinsic velocity of shortening (Spector *et al.* 1980) and a compliant muscle–tendon complex (the tendon length to muscle fibre length ratio is approximately 5; Zajac, 1989; Table 1). As a result, the ability to produce force decreased faster in SO than in GA and PL. For example, if SO was maximally activated during the last third of the support period at a speed of 1.8 m s^{-1} (see Fig. 7), it could produce only about 6–20% of its maximal isometric force (or 2–9 N), because of the very high normalized velocity of shortening of SO muscle fibres during this phase. This result is supported by recent work in which supramaximal stimulation of the soleus nerve during the late phase of support during fast walking in the cat did not produce noticeable increases in SO forces (Herzog and Leonard, 1995). During the late phase of support at a speed of 1.8 m s^{-1} , the estimated values of the contractile abilities of GA and PL were 20–40% (or 41–115 N and 13–37 N, respectively; Fig. 7, Table 1). Therefore, it is speculated that the full activation of SO during the last third of the stance phase at high speeds of locomotion cannot substantially increase the mechanical work done by this muscle and so the observed sharp decrease in muscle activity of SO in this phase (see Fig. 7) may be considered useful.

The decrease in the contractile abilities together with the decrease in the activation of SO cause a fast decrease of force and power relative to the same characteristics of GA and PL during the late phase of support (Figs 2, 7; speeds 1.2 – 1.8 m s^{-1}). Thus, muscles with a high maximum velocity of shortening, a compliant muscle–tendon complex and a high maximum isometric force, such as GA and PL, are better suited to do mechanical work at speeds greater than 0.8 m s^{-1} than are muscles with a low maximum shortening velocity, a stiff muscle–tendon complex and a low maximum isometric force, such as SO. The nervous system may use these features of GA and PL by activating them for a more prolonged period than SO during the late support phase at fast speeds of locomotion (Fig. 7). Because of the activation of GA and the deactivation of SO, and the differences in the contractile abilities between these muscles during the late support phase in fast walking and trotting, the relative contribution of the positive mechanical work of GA to the total positive mechanical work of the major ankle extensor muscles increased and the contribution of SO decreased with increasing speeds of locomotion (Fig. 6).

The relative contributions of the negative work of SO, GA and PL to the total negative work were similar to the corresponding positive contributions (Fig. 6). The only difference was that the negative work of PL was about 15%

of the total negative work. PL contributed only little to the total amount of negative work because this muscle had the smallest absolute elongation during the phase of negative power and PL forces were lower or similar to those of SO during this same period (Figs 2, 4). This pattern of PL force in the early support phase might prevent a premature flexion of the digits. According to Goslow *et al.* (1972), initial contraction of PL causes immediate digit flexion because forces from the plantaris are transmitted 'relatively undiffused' to the tendon of the flexor digitorum brevis to which the tendon of PL is partly attached.

The changes of the SO contribution to the total negative work with increasing speeds of locomotion were opposite to those of GA (Fig. 6). During the period of negative power production in stance, the rates of change in length of SO and GA were similar, the forces of GA increased and the forces of SO did not change substantially (Fig. 2). The increase of GA force during the phase of negative power production with increasing speeds of locomotion might be useful in transferring mechanical energy from the ankle to the knee. Because of this transfer, the knee and hip extensor muscles, having a larger volume than the ankle extensor muscles (and possibly a higher potential to do work), may help the ankle extensor muscles to absorb mechanical energy during the phase of negative power (Prilutsky and Zatsiorsky, 1994; Prilutsky *et al.* 1994b). Also, an increase in force of GA during this phase, with increasing speeds of locomotion, might be useful in increasing the amount of energy stored in the elastic component in series with the contractile component of the muscle (Jewell and Wilkie, 1958; Cavagna, 1970), which may be used during the shortening phase. This action of GA seems to be of advantage for producing mechanical energy, because (1) eccentric muscle contractions require little metabolic energy compared with the corresponding concentric contractions (Curtin and Davis, 1975), and (2) GA is probably better suited to store elastic energy than SO because of its compliant muscle-tendon complex (Alexander and Ker, 1990; Sacks and Roy, 1982; Walmsley and Proske, 1981; Zajac, 1989).

The increase in absolute force and power of PL during the late phase of support during fast walking and trotting may be useful in flexion of the metatarsophalangeal joints (Abraham and Loeb, 1985; Goslow *et al.* 1972). Also, the distance between the knee joint axis and the attachment site on the femur is 2–3 times larger for PL than for GA. This feature gives PL an advantage over GA in using energy generated by the knee extensor muscles to extend the ankle and to flex the metatarsophalangeal joints. This action of multi-joint muscles, sometimes referred to as 'tendon action of multi-joint muscles' (van Ingen Schenau *et al.* 1990), has been associated with human locomotion (Bobbert *et al.* 1986; van Ingen Schenau *et al.* 1990; Prilutsky and Zatsiorsky, 1994), cheetah locomotion (Gambaryan, 1972) and cat locomotion (Prilutsky *et al.* 1994b).

In conclusion, the results of this study suggest that the ankle extensor muscles play a significant role in the generation of mechanical energy for locomotion. During slow walking, SO, GA and PL make similar contributions to the total positive

work done by the three muscles. With increasing speeds of locomotion, the GA contribution increases and the SO contribution decreases because of a faster decrease in the contractile abilities and activity of SO compared with those of GA.

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