

Coordination of medial gastrocnemius and soleus forces during cat locomotion

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Summary

We studied force-sharing behavior between the cat medial gastrocnemius (MG) and soleus (SOL) muscles by direct measurement of the muscle forces and electromyographic activities (EMGs), muscle lengths, speeds of contraction, joint kinematics and kinetics, for a variety of locomotor conditions. Previous studies suggested that the modulation of MG force and activation is associated with movement demands, while SOL force and activation remain nearly constant. However, no systematic, quantitative analysis has been done to evaluate the degree of (possible) modulation of SOL force and activation across a range of vastly different locomotor conditions. In the present study, we investigated the effects of speed and intensity of locomotion on the modulation of SOL force and EMG activity, based on quantitative, statistical analyses. We also investigated the hypothesis that MG forces are primarily associated with MG activation for changing movement demands, while SOL forces are primarily associated with the contractile conditions, rather than activation. Seven cats were trained to walk, trot and gallop at different speeds on a motor-driven treadmill, and to walk up and down different

slopes on a walkway. Statistical analysis suggested that SOL activation (EMG activity) significantly increased with increasing speeds and intensities of locomotion, while SOL forces remained constant in these situations. MG forces and EMG activities, however, both increased with increasing speeds and intensities of locomotion. We conclude from these results that SOL is not maximally activated at slow walking, as suggested in the literature, and that its force remains nearly constant for a range of locomotor conditions despite changes in EMG activity. Therefore, SOL forces appear to be affected substantially by the changing contractile conditions associated with changing movement demands. In contrast, MG peak forces correlated well with EMG activities, suggesting that MG forces are primarily associated with activation while its contractile conditions play a minor role for the movement conditions tested here.

Key words: muscle coordination, contractile condition, medial gastrocnemius muscle, soleus muscle, cat, uphill walking, downhill walking.

Introduction

In search of understanding the force-sharing between synergistic muscles in the control of movement, the medial gastrocnemius (MG) and soleus (SOL) muscles in the cat have been used as the primary experimental model. For almost a quarter of a century the *in vivo* muscle forces and electromyographic (EMG) activities of these muscles have been directly measured by a variety of research groups (Walmsley et al., 1978; Hodgson 1983; Whiting et al., 1984; Gregor et al., 1988; Fowler et al., 1993; Herzog et al., 1993). A consistent finding of these studies was a distinct difference in the division of labor between MG and SOL across a wide range of movement tasks: walking at different speeds or resistances (Walmsley et al., 1978; Hodgson, 1983; Whiting et al., 1984; Gregor et al., 1988, 2001; Pierotti et al., 1989; Fowler et al., 1993; Herzog et al., 1993), standing (Walmsley et al., 1978; Abraham and Loeb, 1985), jumping (Walmsley et al., 1978; Abraham and Loeb, 1985), landing (Abraham and Loeb,

1985) and paw shaking (Smith et al., 1980; Abraham and Loeb, 1985; Fowler et al., 1988). Typically, MG forces and EMG activities correspond to external demands, such as the speed and intensity of movement, while SOL forces and EMG activities seem to remain nearly constant across a range of locomotion speeds, and appear to be independent of external demands. This nearly constant activation of SOL has been associated with a saturation of SOL activation at slow movement (Walmsley et al., 1978; Pierotti et al., 1989), and with a speed-dependent inhibition of SOL activation (Hodgson, 1983) through input from rubrospinal and cutaneous pathways (Burke et al., 1970). SOL EMG activity has been measured and analyzed (see, for example, Walmsley et al., 1978; Gregor et al., 1988; Pierotti et al., 1989) using the time integrated signal, or has been evaluated in a semi-quantitative manner (Hodgson, 1983). However, the results and conclusions of all these previous studies were derived from a

qualitative inspection of results, rather than by systematic, statistical analysis. This is understandable as these measurements are extremely difficult and time consuming to do, so publication of results based on single (Gregor et al., 2001) or a very few animals (Walmsley et al., 1978; Hodgson, 1983; Whiting et al., 1984; Abraham and Loeb, 1985; Gregor et al., 1988; Pierotti et al., 1989; Fowler et al., 1993; Herzog et al., 1993) has been the norm in this area of research. Thus, the mechanisms of control of SOL activity are not well understood, and systematic, quantitative analysis of SOL EMG data are not available at present, but are essential to discuss changes in SOL activation associated with movement demands.

Although the force-sharing between cat MG and SOL has been investigated for a variety of voluntary movements, little is known for steep uphill and downhill walking. SOL forces from a single cat were found to decrease for steep (37°) uphill walking compared to level walking, while MG forces substantially increased under these conditions (Gregor et al., 2001). It was proposed that the decrease in SOL force with increasing uphill slope might be caused by a resultant inhibition of SOL (i.e. smaller EMG activity) through MG force-dependent pathways (Nichols, 1994); however EMG activity was not measured to support this claim. Therefore, in order to confirm the results from a single observation, and to understand why MG forces increase and SOL forces decrease in steep uphill walking, systematic measurements of *in vivo* muscle forces and EMG activity must be made.

It is possible that the contractile conditions (length and rate of change in length) of SOL might play an important role in the production of force, since SOL contractile abilities may be limited under extreme conditions, because of the dominant composition of type S fibers (Burke et al., 1974, 1977). The purposes of this study were: (1) to investigate the effects of speed and intensity of locomotion on the modulation of SOL EMG activity and force based on statistical analysis and (2) to test the hypothesis that cat MG forces are primarily associated

with MG activation, while SOL forces are primarily associated with the contractile conditions, rather than activation. In order to gain novel insight into the mechanism of force-sharing between cat MG and SOL, we performed a comprehensive study under a variety of locomotion conditions, including steep uphill walking conditions (maximally 60°) and galloping, while simultaneously measuring SOL and MG forces, activities and contractile conditions, and the external kinematics and kinetics, so that the external demands could be quantified accurately.

Materials and methods

Cat training

A total of seven outbred, male cats (5.2 ± 1.1 kg) were trained to perform a range of movement tasks: walking at different slopes on a walkway (30° downhill, level, 30, 45 and 60° uphill), walking and trotting at different speeds (0.4 – 1.2 m s⁻¹), and galloping on a motor-driven treadmill. The walking conditions performed successfully by each animal are summarized in Table 1. Training sessions were conducted five times a week for approximately 1 h, for a minimum of 2 months, prior to the surgical implantation of tendon force transducers and EMG electrodes. At the end of each successful training session, rewards (food or brushing) were given.

Muscle force and EMG measurement

Forces in SOL and MG were measured using E-shaped, stainless steel tendon force transducers that were surgically implanted onto the separated tendons of the SOL and MG. The EMG signals of these muscles were measured using indwelling, bipolar fine wire electrodes placed into the mid-belly of SOL and MG. The leads of all force transducers and EMG electrodes were routed subcutaneously to a backpack connector from which all signals were transmitted by telemetry to a custom-built amplifier. Signals were pre-amplified (gain=700 for EMG signals, and a variable, but appropriate,

Table 1. Number of steps analyzed for statistical analysis of muscle force, EMG, muscle length and muscle shortening velocity

Locomotor condition	Force/EMG							Muscle length/speed						
	Cat 1	Cat 2	Cat 3	Cat 4	Cat 5	Cat 6	Cat 7	Cat 1	Cat 2	Cat 3	Cat 4	Cat 5	Cat 6	Cat 7
0.4–0.6 m s ⁻¹	23	43	17	8	17		17	3	39	17	8	17		
Slow speed/level	23	43	17	8	17		17	3	39	17	8	17		
0.8 m s ⁻¹		7		11	22		15					11	22	
1.2 m s ⁻¹			15	17			23				15			
Gallop		16					7							
Fast speed		23	15	28	22		45				15	11	22	
30° downhill	6	8	11	17	16	8		6	8	11	17	16	8	
Downhill	6	8	11	17	16	8		6	8	11	17	16	8	
30° uphill	14	35	38	59	49	43		7	10	11	16	17	12	
45° uphill	22	22	33	38	47	123		4	9	9	18	13	33	
60° uphill	13	18	51		44	18		5	5	12		15	5	
Uphill	49	75	122	97	140	184		16	24	32	34	45	50	

Bold numbers in each row correspond to the total number of steps for each locomotor condition (i.e. slow speed/level, fast speed, downhill and uphill).

gain for each force) and stored on a PC at 2000 Hz. After implantation of the force transducers and EMG electrodes, training was continued one day following surgery. Measurement was carried out when cats had completely recovered from surgery, such that kinematics and kinetics (ground reaction force and resultant joint moment) of the implanted hindlimb were similar to those obtained before surgery. This typically happened 1 week following implantation of the force transducers and EMG electrodes. For a detailed description of the surgical procedures, the measurement of tendon forces and the recording of muscular EMGs, see Herzog et al. (1993).

Kinematic and kinetic measurements

Five reflective markers (10 mm diameter) were placed over the hip, knee, ankle, metatarsophalangeal (MP) joint and toe of the instrumented hindlimb, to obtain knee, ankle and MP joint angles. For level, uphill and treadmill walking, the three-dimensional positions of these markers were collected by a motion analysis system (60 Hz; VP310, Motion Analysis Cooperation, Santa Rosa, CA, USA). For downhill walking, movements were videotaped using a high-speed camera (200 Hz; V-14B, NAC, Inc., Tokyo, Japan), and markers were manually digitized using a custom-designed program written in MATLAB (Math Works, Inc., Natick, MA, USA). In order to avoid errors caused by skin marker movement, the location of the knee joint center was calculated using an optimization procedure, in which the estimated location of the knee joint center was optimized to be closest to the measured location of the knee marker, with the constraint that the distances from the estimated knee joint center to the measured ankle and hip joint were the same as the measured shank and thigh length, respectively. This optimization was performed using the MATLAB function, 'fmincon' (Math Works, Inc., Natick, MA, USA). In order to synchronize the kinematic data with the muscle force and EMG data, a synchronization pulse was sent from the motion analysis system to the computer when data acquisition was started. For synchronization of the high-speed video images with the muscle force and EMG data, a series of voltage pulses was sent to the computer simultaneously with a light emitting diode (LED) pulse that was recorded on the video images.

For downhill, level and uphill walking, ground reaction forces (GRFs) of the instrumented hindlimb were measured using two force platforms located in the center of a walkway (DRMC36, AMTI, Newton, MA, USA). GRFs were stored simultaneously with the muscle forces and EMG signals on a computer at 2000 Hz. All procedures were approved by the Life Sciences Animals Ethics Committee of the University of Calgary.

Joint moment, EMG and muscle length analysis

In order to identify the stance phase of locomotion, the instants of paw-contact and paw-off were identified using the GRFs, when available, or the video images. The resultant joint moments at ankle and knee were calculated using the inverse

dynamics approach (Andrews, 1995) with hindlimb kinematics and GRFs as input.

The amplified EMG signals were high-pass filtered with a cut-off frequency of 15 Hz, and full-wave rectified. The EMG data were further processed to determine the onset and offset of activation using a criterion based on a minimum threshold of three standard deviations above the resting baseline for each muscle (Neptune et al., 1997). The magnitude of activation was quantified using the average root mean square (RMS) values of the full-wave rectified EMG between the onset and offset of activity, as recommended by Basmajian and De Luca (1985).

Muscle-tendon lengths of MG and SOL were calculated using the joint kinematics, obtained during free locomotion and the tendon travel technique (Grieve et al., 1978) after all data collection was completed. Speeds of muscle shortening were calculated as the first time derivative of muscle-tendon length using a quintic spline function (GCVSPL; Woltring, 1986).

Statistical analyses

In order to understand the effect of speed and intensity of locomotion on peak muscle force, EMG activity, muscle-tendon length, and shortening speed for MG and SOL, means of these variables from consecutive step cycles were compared across walking conditions using a repeated-measures analysis of variance (RM-ANOVA; SPSS Inc., Chicago, IL, USA). For analyses of the peak muscle force and EMG activity, steps for which kinematic data were not available were also included. The number of walking steps for the determination of the peak muscle force and EMG activity was therefore greater than that used for the determination of the muscle-tendon length and shortening speed (Table 1). The peak muscle force and the RMS value of EMG activity were normalized relative to the mean value for slow treadmill walking ($0.4\text{--}0.6\text{ m s}^{-1}$), except for cat6, whose data were normalized relative to the mean value for level walking on the walkway, since this animal did not perform treadmill walking. SOL forces for cat3 and cat4 were not available, due to transducer failure.

In order to distinguish between the effects of speed and intensity on EMG activity and muscle force, a RM-ANOVA was performed separately for the level treadmill walking conditions, for which speed was well controlled, and the sloped walking conditions, for which speed was controlled in a *post-hoc* manner through the stance times. For treadmill walking, not all animals walked at the same speeds (Table 1). Therefore, the number of animals varies for a given speed condition. The mean values for slow treadmill walking ($0.4\text{--}0.6\text{ m s}^{-1}$; $N=6$) were compared to the mean values for fast treadmill walking ($>0.6\text{ m s}^{-1}$; $N=5$). For level, uphill and downhill walking, data were obtained from six animals for all conditions, except that the steepest uphill condition (60°) was only performed by five animals (Table 1). The mean values of the target variables for $0.4\text{--}0.6\text{ m s}^{-1}$ level walking were compared with the downhill and uphill walking conditions (30 , 45 and 60°).

In order to investigate whether peak SOL forces and EMG activities decrease with increasing MG forces and EMG activities from level to uphill walking, as suggested by Gregor

et al. (2001), correlation coefficients between the normalized peak SOL and MG force, and between the normalized SOL and MG EMG activity were calculated for consecutive steps, while animals walked on the level part of the walkway before

walking up the sloped walkway, and then as they walked on the level surface at the top of the sloped part of the walkway. The numbers of walking steps for each level–uphill–level walking condition (30, 45 and 60°) are summarized in Table 2.

Table 2. Correlation coefficients between the normalized peak MG and SOL forces and between the normalized MG and SOL root mean squares of electromyographic (EMG) activity for uphill walking

Walking angle*	Correlation coefficient		Number of steps				
	MG–SOL force	MG–SOL EMG	Cat 1	Cat 2	Cat 5	Cat 6	Total
30°	–0.50	0.24	15	21	22	26	84
45°	–0.61	0.58	10	16	19	36	81
60°	–0.56	0.43	23	19	26	12	80

*Uphill walking at 30°, 45° and 60°.

Data were analyzed from consecutive steps obtained from several walking trials. The number of steps from each animal are given.

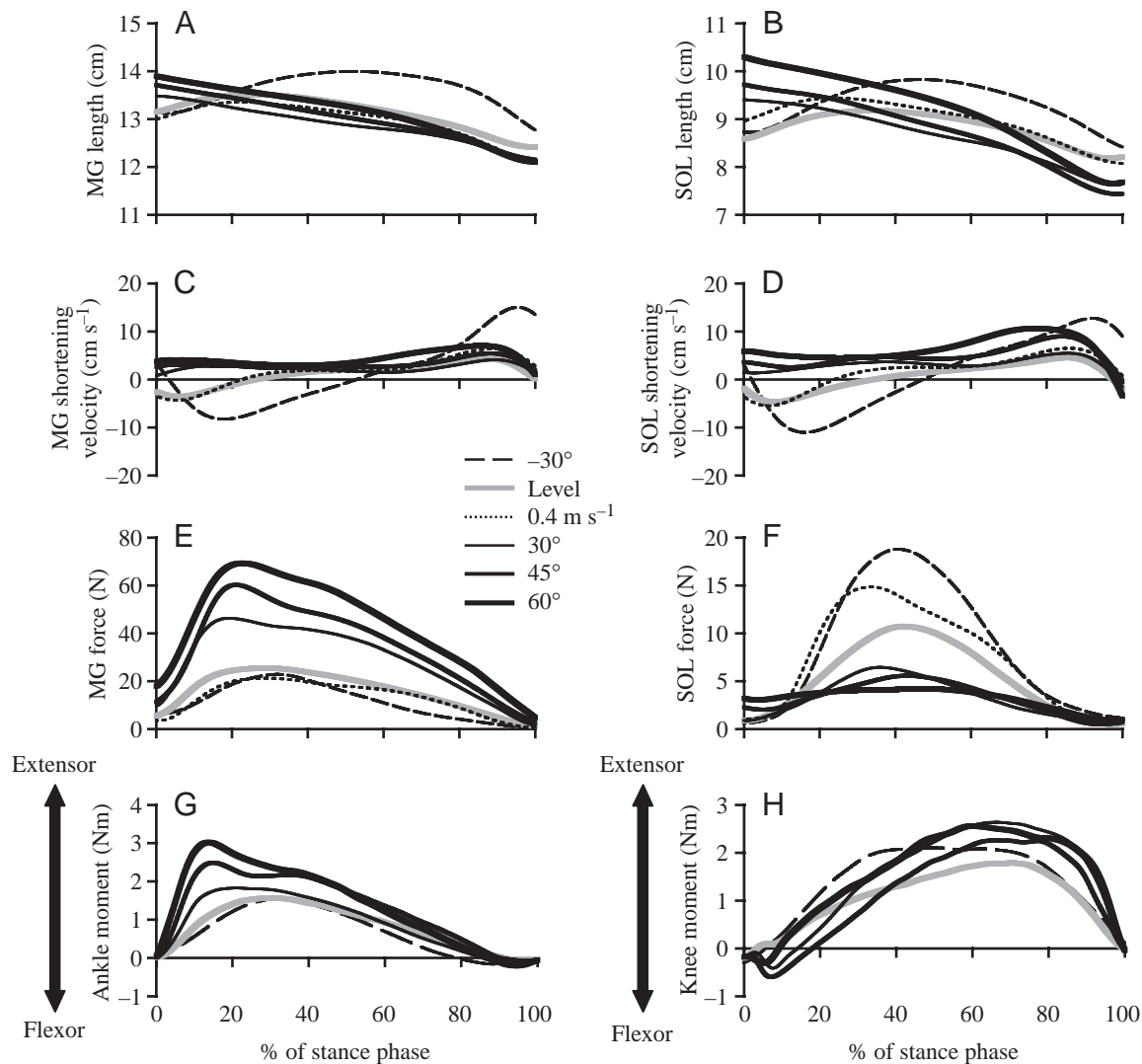


Fig. 1. Mean time-histories of selected variables from a single animal normalized to the total stance time for a variety of locomotor conditions. (A) MG muscle–tendon length, (B) SOL muscle–tendon length, (C) MG velocity, (D) SOL velocity (shortening is positive, stretching is negative), (E) MG muscle force, (F) SOL muscle force, (G) resultant ankle joint moment (extensor moments are positive, flexor moments are negative), (H) resultant knee joint moment (extensor moments are positive, flexor moments are negative).

Results

General results

The initial muscle-tendon lengths of MG and SOL were longer for uphill walking trials than those for downhill, level, and treadmill walking trials (Fig. 1A,B), because the cats were more crouched at the beginning of upslope compared to level and downhill walking. For downhill walking, MG and SOL lengthened up to about the middle of the stance phase. For level and treadmill walking, lengthening in the first part of the stance phase was followed by shortening for the remainder of stance for both MG and SOL. In contrast to downhill and level walking, MG and SOL shortened over the entire stance phase of uphill walking, because of the pronounced and continuous ankle plantar flexion during this phase. Muscle elongation and shortening (and therefore the total excursion) during locomotion was typically greater for SOL than for MG (Fig. 1A,B).

MG forces were greater for uphill walking than those for any of the other walking conditions (Fig. 1E). In contrast, SOL forces for the different animals were either similar or smaller for uphill than those for the other walking conditions (Fig. 1F). The ankle plantar flexor moments increased from level to uphill walking (Fig. 1G), thus MG forces increased with increasing movement demands, whereas SOL forces did not. However, not only the changes in magnitude, but also the MG force-time histories for the entire stance phase (Fig. 1E) were similar in shape to the ankle moment curves (Fig. 1G), whereas the SOL force-time curves (Fig. 1F) bore little resemblance to the ankle moment curves (Fig. 1H).

Peak MG forces increased significantly from slow walking (0.4–0.6 m s⁻¹) to fast walking (0.8–1.2 m s⁻¹) and galloping, and also increased significantly from downhill to level, and

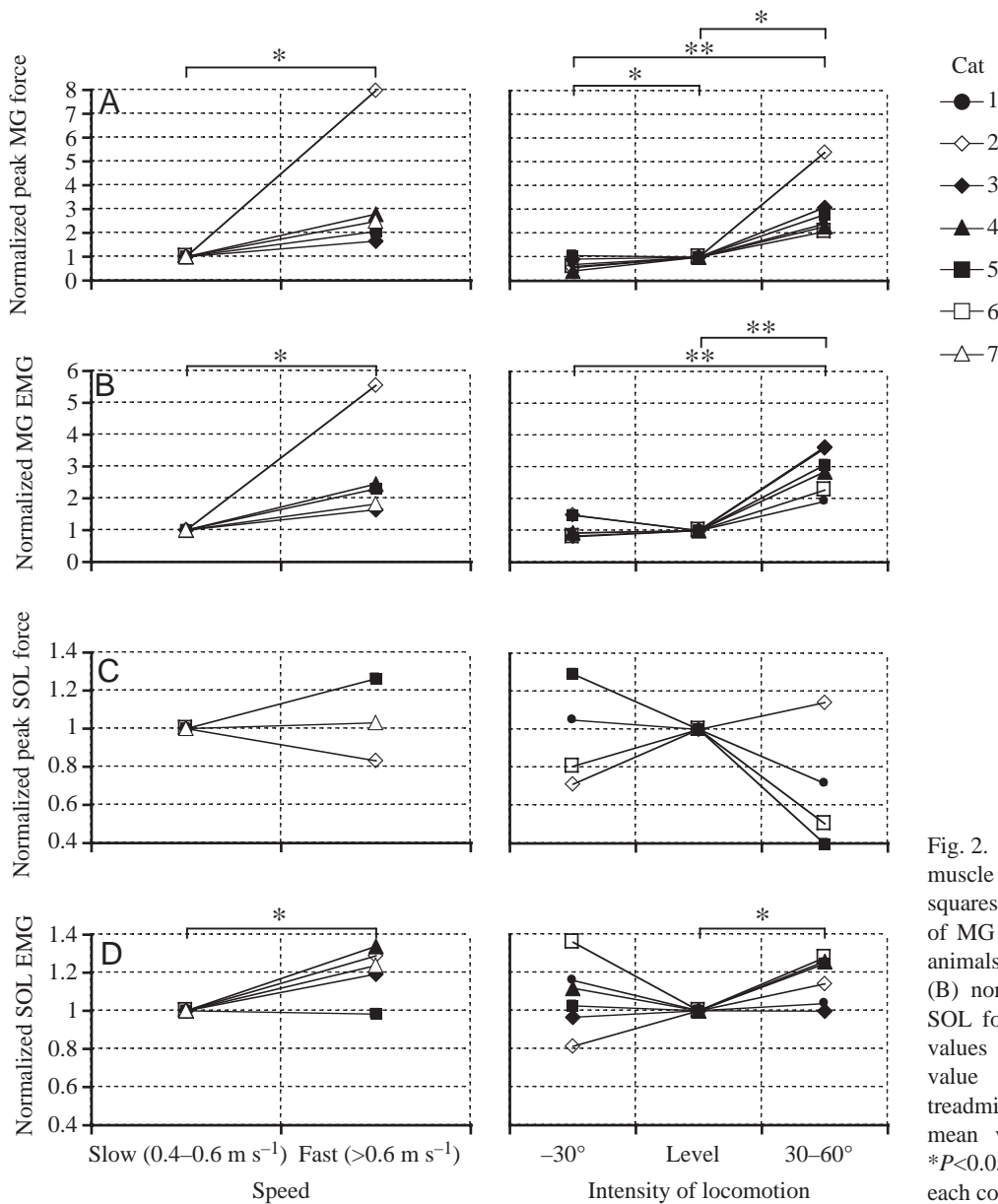


Fig. 2. Mean values of normalized peak muscle force and normalized root mean squares of electromyographic activity (EMG) of MG and SOL for all seven experimental animals. (A) Normalized peak MG force, (B) normalized MG EMG, (C) normalized SOL force, (D) normalized SOL EMG. All values are normalized relative to the mean value obtained at 0.4–0.6 m s⁻¹ level treadmill walking for cats 1–5 and 7, and the mean value of level walking for cat 6. **P*<0.05; ***P*<0.01; the numbers of steps for each condition are given in Table 1.

uphill walking (Fig. 2A). These increases in MG force were associated with increases in EMG activity (Fig. 2B). In contrast, the mean SOL peak forces did not change (Fig. 2C), while SOL EMG activity significantly increased with increasing speeds and intensities of locomotion (Fig. 2D). The increase in normalized peak force and EMG activity across all locomotor conditions was 8 and 6 times for MG (Fig. 2A,B) and approximately 1.4 and 1.4 times for SOL, respectively (Fig. 2C,D).

The relationships between the peak muscle forces and the corresponding RMS values of the EMG for MG and SOL are shown in Fig. 3 for downhill, level+treadmill ($0.4\text{--}1.2\text{ m s}^{-1}$),

and uphill walking, as well as galloping. MG peak forces and EMG activities had a strong positive correlation for all animals ($r^2=0.66\text{--}0.90$), while SOL peak forces and activities were not correlated in a systematic way (positive and negative regression slopes, $r^2=0.03\text{--}0.17$).

Coordination of MG/SOL force and activation between level and uphill walking

In consecutive step cycles of uphill walking, SOL forces were small when MG forces were great, and *vice versa* (Fig. 4). Systematic analysis revealed that the peak MG and SOL forces

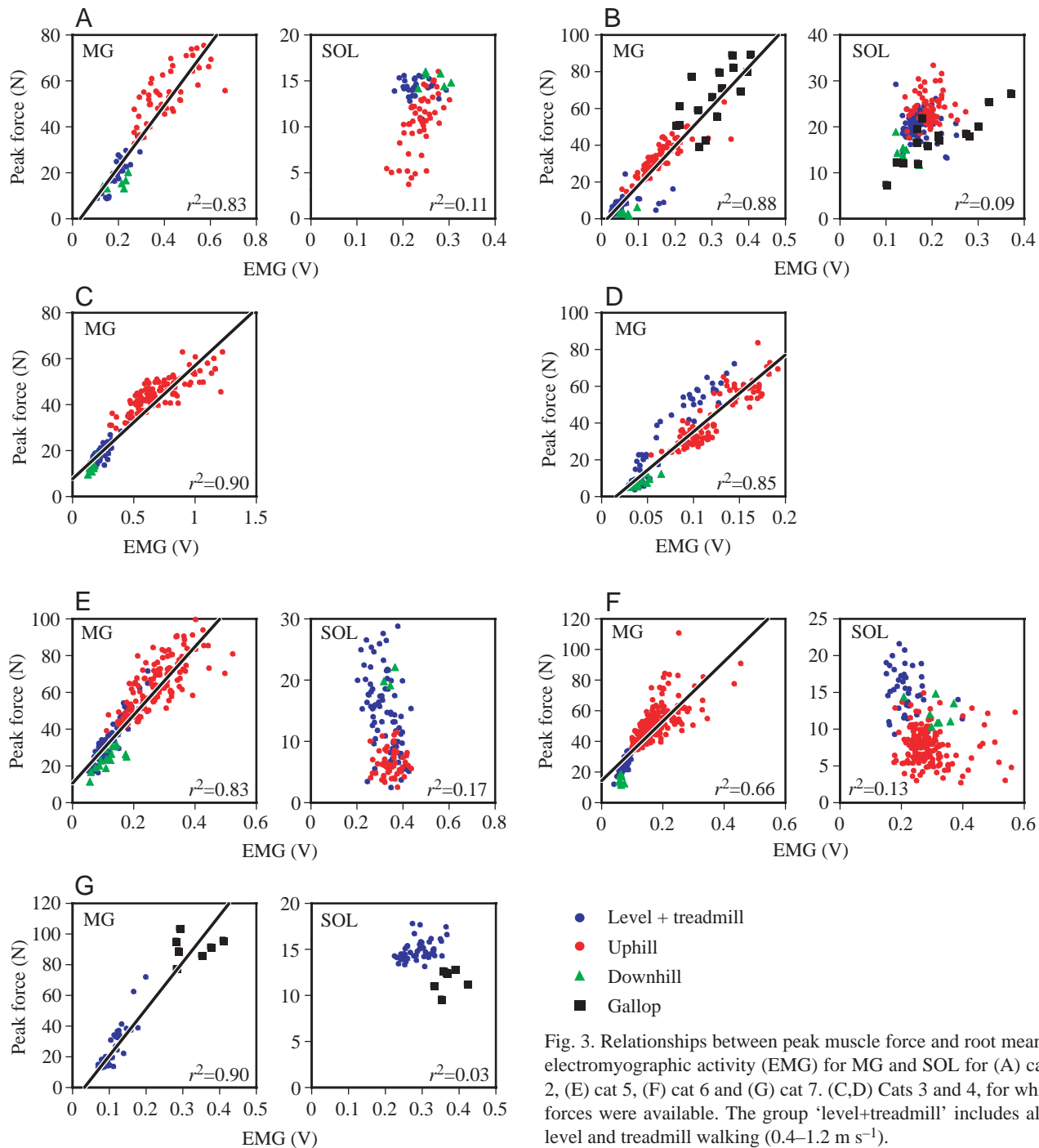


Fig. 3. Relationships between peak muscle force and root mean squares of electromyographic activity (EMG) for MG and SOL for (A) cat 1, (B) cat 2, (E) cat 5, (F) cat 6 and (G) cat 7. (C,D) Cats 3 and 4, for which no SOL forces were available. The group 'level+treadmill' includes all data from level and treadmill walking ($0.4\text{--}1.2\text{ m s}^{-1}$).

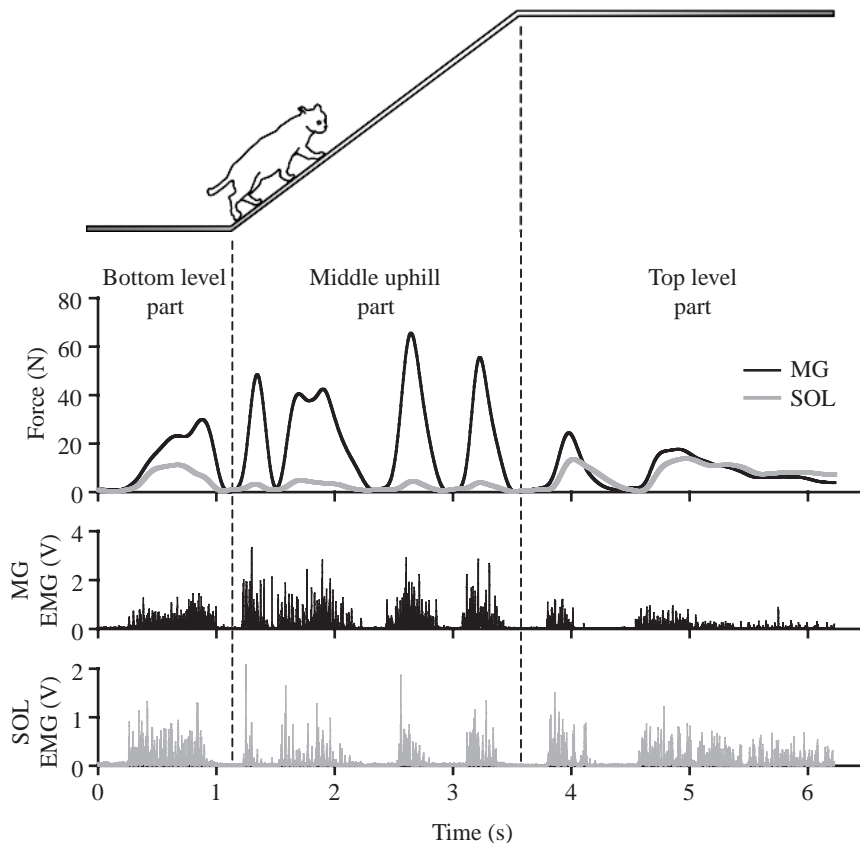


Fig. 4. Example of MG and SOL forces and electromyographic (EMG) activities for consecutive step cycles of uphill walking (60°) on a walkway. Cats made a step or two at the bottom, level part of the walkway, then walked up the sloped part of the walkway, and finally performed a few more steps on the top, level part of the walkway.

were negatively correlated ($r=-0.50$ for 30° ; $r=-0.61$ for 45° ; and $r=-0.56$ for 60° ; Fig. 5 and Table 2), while the corresponding EMG activities were positively correlated ($r=0.24$ for 30° ; $r=0.58$ for 45° ; and $r=0.43$ for 60° ; Fig. 5 and Table 2), indicating that greater activation of MG, and greater force in MG, were associated with increased SOL activation, but decreased SOL force.

Changes in contractile conditions

Muscle stretching from paw contact to the instant of peak muscle force (stretching is negative; Fig. 6) was significantly greater for downhill than for level and uphill walking. This difference in muscle excursion was associated with significant differences in the instantaneous velocity of shortening at the instant of peak force production (stretching is negative; Fig. 7). For all cats, MG and SOL were stretched at the instant of peak force production for downhill walking, they were about isometric for level walking, and were shortening for all animals for the uphill walking conditions (Fig. 7).

Discussion

The force-sharing problem is arguably the most basic problem in motor control, and is one of the great challenges for internal force analysis in biomechanics. The cat SOL and MG muscles are the primary experimental model for studying the force-sharing between synergistic muscles. Based on previous work, MG forces are known to increase with

increasing movement demands, as one might expect (Walmsley et al., 1978; Hodgson, 1983; Fowler et al., 1993; Herzog et al., 1993; Gregor et al., 2001), while SOL forces seem to remain constant across a variety of locomotor speeds (Walmsley et al., 1978; Hodgson 1983; Fowler et al., 1993; Herzog et al., 1993), and have been shown to decrease in a single animal for steep uphill walking (Gregor et al., 2001). There is no convincing explanation for why SOL forces remain constant, or decrease, for increasing movement speeds and demands. It has been speculated that SOL may be inhibited, and therefore its activity may be reduced, either through speed-dependent (Hodgson, 1983) or MG force-dependent pathways (Nichols, 1994; Gregor et al., 2001) that may (at least partly) offset possible increases in excitatory drive. However, these suggestions were not based on quantitative analysis, probably because it is extremely difficult and time consuming to obtain sufficient data for statistical analysis, and also because relevant data were often missing (e.g. EMG was not recorded in the study by Gregor et al., 2001). Here, we add quantitative results and statistical analyses to existing qualitative interpretations on SOL and MG force-sharing for some widely studied conditions (level walking), and some conditions (uphill/downhill walking, galloping) for which little or no information is available.

Effect of speed and intensity of locomotion on the modulation of SOL force and EMG activity

SOL EMG activity significantly increased with increasing speeds and intensities of locomotion (Fig. 2D). Hence, the net

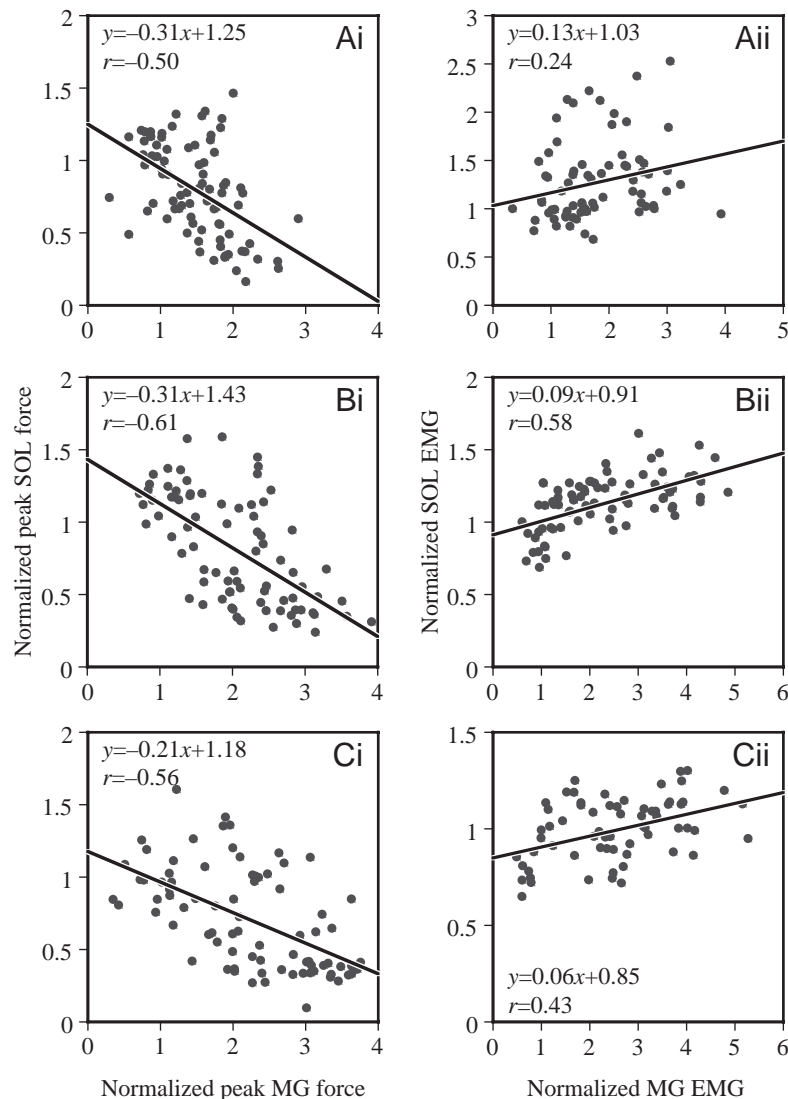


Fig. 5. Best-fit linear correlations between the normalized peak MG and SOL forces (Ai–Ci), and between the normalized MG and SOL root mean squares of electromyographic activity (EMG) (Aii–Cii) for consecutive step cycles of uphill walking in four animals. (A) 30°, (B) 45°, (C) 60°. The correlation coefficients, and the total number of steps for these trials, are summarized in Table 2.

change in SOL activity (excitation and inhibition) was excitatory for fast walking/trotting, galloping and uphill walking compared to slow walking. In contrast, SOL peak forces were found to remain constant for the conditions tested here. The force results are consistent with previous studies, which suggested that SOL peak forces remain nearly constant for a wide range of walking and trotting speeds (Walmsley et al., 1978; Hodgson, 1983). This result has been interpreted as a saturation of SOL activation at low speeds of locomotion (Walmsley et al., 1978; Pierotti et al., 1989). However, we found a statistically significant increase in SOL activation with increasing speeds and intensities of locomotion, suggesting that SOL activation is not maximal (or saturated) at slow

speeds of walking. Similarly, Walmsley et al. (1978) showed a dramatically increased SOL EMG during the take-off phase of jumping compared to all locomotor conditions (their fig. 8), thereby providing strong evidence against their own argument that SOL activation was maximal at slow speeds of walking. Therefore, we conclude that SOL is not fully activated at slow speeds of walking. Of course, our results do not exclude the possibility of SOL inhibition through speed- (Hodgson, 1983) or force-dependent pathways (Nichols, 1994; Gregor et al., 2001). However, any such inhibition would be offset by an even greater excitation associated with increased movement demands. Our results also do not exclude the possibility that a net speed-dependent inhibition might exist for movements performed at greater speeds than galloping, for example, during a paw shake or a scratch response; i.e. movements that are performed at frequencies of 5–10 Hz (Smith et al., 1980; Abraham and Loeb, 1985; Fowler et al., 1988; M. Kaya, T. Leonard and W. Herzog, unpublished observations).

It has been suggested that SOL activity is strongly inhibited by increasing MG force in decerebrate cats (Nichols, 1994). This force-dependent inhibition of SOL has been used by Gregor et al. (2001) to explain the decrease in SOL force with increasing MG force for uphill walking compared to level or downhill walking. Our results did not show a statistically significant decrease in SOL force from level (0.4–0.6 m s⁻¹) to uphill walking, although three out of the four animals for which force recordings were available in our study, showed substantial decreases in the peak SOL forces, as did the single animal tested by Gregor et al. (2001). Also, peak SOL and MG forces were negatively correlated for consecutive step cycles of uphill walking (Fig. 5). Thus, our results are consistent with those of Gregor et al. (2001), and they suggest that increasing MG forces are typically associated with decreasing SOL forces. However, SOL activity increased

significantly with increasing MG activity (Fig. 5) and MG force (not shown) for all uphill walking conditions, suggesting that SOL forces did not remain constant (one animal) or decrease (three animals) because of a decrease in activation, but despite a net increase. Again, our measurements do not distinguish between inhibitory and excitatory signals to SOL. Thus, a strong MG force-dependent inhibition (Nichols, 1994) may have been present in SOL for the uphill walking conditions, but this inhibition (if present) was offset by an even greater increase in excitation. Unfortunately, the only other force data for uphill walking (Gregor et al., 2001) cannot be used for resolving this issue, as no EMG data were collected in that work.

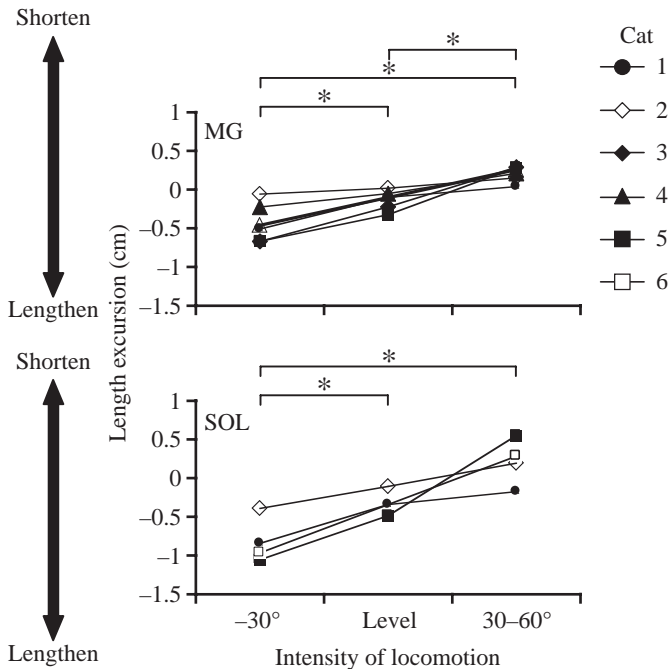


Fig. 6. Mean values of muscle-tendon excursion of MG and SOL from the instant of paw contact to the instant of peak muscle force (positive values represent muscle shortening, negative values represent muscle lengthening). Level=0.4–0.6 m s⁻¹. *P<0.05; the number of steps for each locomotion condition is given in Table 1.

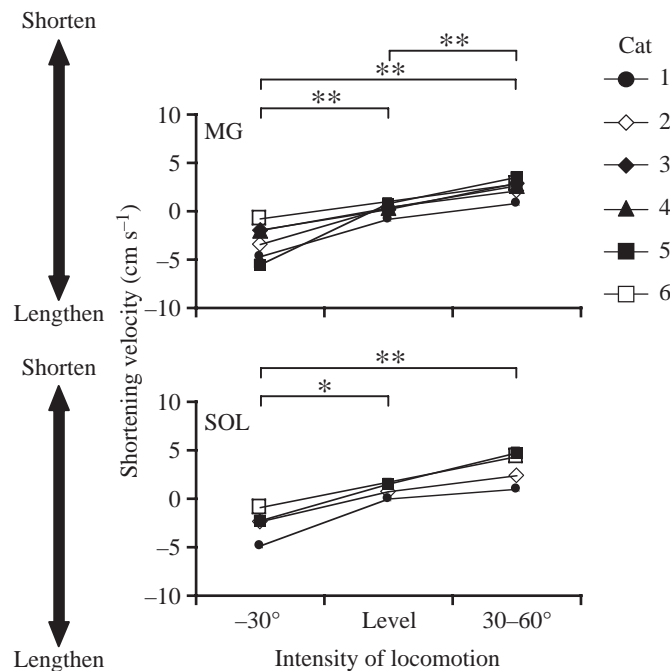


Fig. 7. Mean values of the instantaneous velocity of shortening of MG and SOL at the instant of peak muscle force (positive values represent muscle shortening, negative values represent muscle lengthening). Level=0.4–0.6 m s⁻¹. *P<0.05; **P<0.01; the number of steps for each locomotion condition is given in Table 1.

MG force depends primarily on MG activation, while SOL force primarily depends on SOL contractile conditions

The instantaneous force in any muscle depends on the degree of activation (e.g. Rack and Westbury, 1969) and the contractile conditions (e.g. length, Gordon et al., 1966; velocity, Hill, 1938; history, Abbott and Aubert, 1952). In this study, we found that peak MG forces and EMG activities increased with increasing speeds and intensities of movement (Fig. 2), and that they were strongly correlated for all animals (Fig. 3). These results suggest that MG forces are primarily associated with MG activation, and are not greatly influenced by the contractile conditions (at least not for the movements tested here). In contrast, SOL forces were not systematically correlated with EMG activity (Figs 2 and 3). This tendency is exemplified in Fig. 5, where peak SOL forces decreased with increasing SOL activity. These results suggest that SOL forces are influenced to a great degree by the contractile conditions, and that the increases in SOL activity with increasing movement demands keep SOL forces constant in the presence of less favorable contractile conditions (i.e. increasing speeds of shortening for uphill compared to level and downhill walking; Fig. 7).

MG and SOL are stretched from paw contact to the instant of peak muscle force for downhill and level walking, while they shorten for uphill walking (Fig. 6). This active lengthening of SOL for downhill and level walking enhances SOL force production because of the active lengthening of the muscle and the force-velocity properties (Hill, 1938). Thus, the substantial decrease in peak SOL force, despite an increase in activation, for uphill walking compared to level walking found in three animals (Fig. 2) is probably associated with the increase in SOL shortening velocity for the uphill compared to the level walking conditions.

Modulation of MG and SOL coordination

Changes in the amplitude of peak force and EMG activity for a range of movements were different between MG and SOL. MG peak force and EMG activity increased 2–8 times from slow walking (0.4–0.6 m s⁻¹) to fast walking, trotting, uphill walking, or galloping. Changes in the peak SOL force and EMG activity were within about ±50% of that for slow walking (Fig. 2). MG is primarily composed of fast-twitch fibers (Burke et al., 1977) and has a maximum isometric force capacity of about 100 N (Spector et al., 1980; M. Kaya et al., unpublished results). The 15–20 N of MG force during slow walking is only about 15–20% of the isometric force capacity, therefore MG's force and activation is only a small percentage of its full potential. In contrast, SOL is primarily composed of slow-twitch fibers (Ariano et al., 1973; Burke et al., 1977) and has a maximum isometric force capacity of about 30 N (Spector et al., 1980; Herzog et al., 1992; Scott et al., 1996). Therefore, the 15–20 N of SOL force during slow walking constitutes a substantial percentage (≥50%) of SOL's potential. Therefore, a substantial increase in SOL force above that obtained for slow walking is only possible if activation goes

towards maximum, or if the muscle is stretched at full activation. Although the size principle of motor unit recruitment is not applicable across muscles, but only within a given muscle (see paw-shake response in cat SOL and MG; Smith et al., 1980; Abraham and Loeb, 1985), it is feasible to assume that the 95–100% slow SOL is recruited to a much greater extent for standing and slow walking than the 70–80% fast MG. Consequently, there is less room for SOL force and activity modulation from the slow walking baseline, compared to MG force and activity modulation.

Mechanical interpretation of MG and SOL

As shown in Fig. 1, the MG force–time curves were similar in shape to the resultant ankle joint moment curves, whereas the SOL force–time curves showed little resemblance to them. These results suggest that MG force production is closely related to the ankle extensor moments, whereas SOL force production appears to be largely independent of these moments. Gregor et al. (2001) suggested that uphill walking constitutes an ideal situation for the two-joint MG, because the initial phase of uphill walking is associated with a knee flexor and an ankle extensor moment (Fig. 1G,H). However, careful analysis reveals that MG forces and ankle extensor moments increase systematically with increasing slopes of uphill walking, but knee flexor moments do not (Fig. 1E,H). Therefore, our results are consistent with the idea that MG acts like an ankle extensor with little regard to satisfying movement demands at the knee.

Conclusion

Cat SOL EMG activity significantly increases with increasing speeds and intensities of locomotion, whereas SOL forces tend to remain constant in these situations. These results do not support the idea of a saturation of SOL activation at slow movements (Walmsley et al., 1978), nor do they support the notion that constant SOL forces are associated with constant activation caused by speed-dependent inhibition of SOL activation for increasing walking speeds (Hodgson, 1983). Moreover, a negative correlation between SOL and MG peak forces during uphill walking was associated with a positive correlation between SOL and MG activations. Thus, these results do not support the idea of a MG force-dependent inhibitory pathway on SOL activation (Nichols, 1994) to explain the experimentally observed decrease in SOL force during uphill compared to level walking (Gregor et al., 2001). Although it cannot be excluded that SOL is inhibited through such pathways for uphill walking, excitatory signals more than offset any such inhibitory signals. As hypothesized, SOL forces are affected to a great extent by SOL contractile conditions, and SOL activation during locomotion seems to be regulated in such a way that changes in force associated with changes in contractile conditions are largely offset to maintain SOL force approximately constant. In contrast to SOL, MG activity and force increase with increasing external demands and show a strong statistical correlation, suggesting that MG

contractile conditions play a minor role in force production for the movements studied here. MG forces closely follow MG activation. The decrease in SOL force with increasing levels of activation observed for high intensity movements such as jumping (Walmsley et al., 1978) begs the question of whether SOL is eventually deactivated when movement speeds become so fast that SOL forces would become very small, even if fully activated? And if so, the pathways responsible for SOL deactivation would need to be found to understand in detail the intricate nature of the force-sharing behavior between these two muscles, specifically, and synergistic muscles, in general. These questions will need careful investigation in the future.

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