Forces Produced by Medial Gastrocnemius and Soleus Muscles During Locomotion in Freely Moving Cats

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SUMMARY AND CONCLUSIONS

1. Force transducers designed for chronic implantation were placed on the individual tendons of the medial gastrocnemius (MG) and soleus (SOL) muscles in the same hindlimb of adult cats. Electromyographic (EMG) and kinesiological data were also recorded. Force, EMG, and movement data obtained from intact, freely moving cats illustrate the division of labor between the mixed MG and its slow-twitch synergist SOL during posture, treadmill locomotion, and jumping.

2. Throughout a wide range of speeds, from slow walk (0.6 m/s) to fast run (3 m/s), the SOL develops approximately the same peak force (between 1.6 and 2.0 kg wt, depending on the animal) while the average MG force varies over a threefold range (from about 0.6 to 2.0 kg wt). However, even during fast running, the SOL can produce as much, or more, peak force as the MG.

3. In quadrupedal standing, the SOL can at times produce as much force as during locomotion, but on the average, SOL output is somewhat less (about 1.2–1.4 kg wt). In contrast, the MG usually produces no more than 0.5 kg wt of force during quiet standing.

4. Vertical jumping, up to a maximum height of 120 cm, involves peak MG forces up to about 9 kg wt (average approximately 8.0 kg wt), which can be 10–15% greater than the maximum isometric force developed by the same muscle during fused tetanic contraction (stimulus rate >100 Hz) at optimum length.

5. During the step cycle the peaks of both MG and SOL force profiles occur before the end of the yield (E2) phase, as both muscles undergo active lengthening. In contrast, peak MG and SOL forces during vertical jumping coincide with the end of active lengthening and the onset of ankle extensor shortening.

6. The results are consistent with the hypothesis that the inherent stiffness of active muscle during the step cycle is an important factor in the control of force output from hindlimb extensor muscles in locomotion. The division of labor between MG and SOL and the absolute force levels required from the MG during the full range of hindlimb movements in posture, locomotion, and jumping appear to be precisely matched to the very different characteristics of the motor-unit populations composing these synergistic muscles.

INTRODUCTION

Studies of the neural control of locomotion necessarily involve some quantitation of motor output. Although this is usually done in terms of the resultant movement itself or of patterns of electrical activity in selected muscles, Manter (22) in 1938 measured the force vectors produced by hindlimbs of cats during locomotion. Using these data, Grillner (18) made estimates of the forces developed by the triceps surae muscles during walking and standing. Burke, Rymer, and Walsh (10) extrapolated Grillner's results once more to arrive at estimates of the force contributed by the MG muscle alone during locomotion in
In order to compare these with the properties of MG motor units, we have developed a chronically implanted force transducer system to measure directly the force produced by individual ankle extensor muscles in unrestrained moving cats.

The results illustrate the division of labor between the MG and its slow-twitch synergist, the SOL, during postural activity, walking, and running on a treadmill and vertical jumping. The SOL muscle of the cat often develops as much force during quiet standing as it does throughout the entire range of locomotion from slow walk to fast run. In contrast, MG generates only small forces during standing, but contributes a major fraction of the wide dynamic range of peak force output required during locomotion at different speeds, and particularly during jumping.

METHODS

Force transducer manufacture and calibration

The transducer substrate was cut from stainless steel sheet (316 alloy) and hand filed into the rounded letter E shape illustrated in Fig. 1A. This shape is a modification of the "belt buckle" transducer design suggested some years ago by Salmons (28). A semiconductor strain gauge (BLH type SPB1-12-35) was then bonded along one side of the substrate with light pressure, using epoxy cement (Devcon EK-20). Teflon-insulated stranded stainless steel wires (Bergen Wire Rope Co. BWR 3.48) were soldered to the

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**Fig. 1.** A: photograph of the transducer assembly (en face view above), indicating placement of semiconductor strain element, lead wires, and position of tendon (shading). Lower diagram shows longitudinal section with tendon (stippled) threaded through the gauge. B: calibration curves for typical gauge showing bridge voltage output (ordinate) versus force (abscissa) during static test (weight on string) and during twitch and tetanus of MG muscle with same gauge in situ on MG tendon (see text).
Implanting resistance was quite temperature sensitive, the was also studied. Although the strain element gauge factor varied negligibly over the range tested (lo-50°C). It was concluded that the static measurements obtained by suspending weights from the tendon. In addition, a static calibration was therefore checked in a terminal experiment under pentobarbital anesthesia with the gauges in situ. The purpose of the Silastic rubber (Dow-Corning medical adhesive silicone type A) was then coated over the transducer and two slits cut in the side (opening of the F) to allow the gauge to be placed on the intact tendon. The transducer operates by measuring the strain in the stainless steel substrate induced by tension in the tendon. The gauge was used in a simple DC Wheatstone bridge arrangement. (The nominal resistance of the gauges used was 350 Ω.)

A static calibration for the transducer was obtained by placing the gauge on a string and suspending various weights. Figure 1B shows the static calibration curve for one transducer. Although semiconductor strain gauges are inherently nonlinear, the dimensions of the stainless steel substrate were chosen such that the transducers were reasonably linear over the force range of interest (up to 10 kg wt). Adaptation of the design for larger forces and different tendon dimensions should be possible. The linear least-squares regression line (of the form y = ax) on the graph in Fig. 1B shows that this particular gauge was quite linear up to 10 kg wt. It was found that the calibration curve for a given transducer depended to some extent on the thickness of the calibrating string. Each calibration was therefore checked in a terminal experiment under pentobarbital anesthesia with the gauges in situ on their tendons. To do this, the appropriate tendon was cut distally to the transducer and tied to a Grass strain gauge (type PT-10). The muscle nerve was then dissected free and stimulated. A calibration curve was obtained for both graded single twitches and tetani, as shown in Fig. 1B. In addition, a static calibration was obtained by suspending weights from the tendon. It was concluded that the static measurements produce an adequate calibration curve for each transducer.

The effect of temperature on the transducer was also studied. Although the strain element resistance was quite temperature sensitive, the gauge factor varied negligibly over the range tested (10–50°C).

Implanting

Force transducers and EMG electrodes were implanted in the left hindlimb under aseptic conditions. The SOL tendon is clearly separable from those of LG and MG and the SOL transducer was slipped onto it, in series with SOL alone. The MG and LG tendons are formed from broad aponeuroses, but the tendon fibers that transmit force from each muscle can be identified at a point 3-4 cm proximal to the calcaneus. They were split from this point to the calcaneus and the MG transducer was slipped onto the MG portion, as in Fig. 1A.

Bipolar EMG wires (Teflon insulated, stranded stainless steel) were inserted into the central portions of the MG and SOL muscles and kept in place with sutures. The MG electrodes were placed into regions of the muscle in which the distribution of histochemical muscle fiber types is representative of the whole muscle (9). All lead wires were then passed subcutaneously to a connector on the cat's back, and a ribbon cable was used to carry the signals to the recording apparatus.

Recording

The cats were trained to walk and run on a treadmill and to jump vertically from the floor onto a table in order to receive food rewards. The EMG and force data were recorded onto FM tape, and a strobbed (60 Hz) videotape record was taken of the cat's movements. The FM and videotapes were synchronized with the use of an IRIG-B code timer whose output was recorded onto both tapes.

In order to determine joint angles and muscle lengths, reflective spots were placed over the iliac crest, great trochanter, lateral malleolus at the ankle, and the distal foot. Joint angles were measured using these spots and muscle lengths were then calculated from these measurements taken from successive single frames of the video record, using the trigonometric method of Goslow et al. (16). (Measurements of the distances between pivot points and the points of origin and insertion of the muscles were taken when the cat was sacrificed.) In later experiments, length gauges similar to those used by Prochazka et al. (26) were implanted along the MG muscle, from femoral condyle to calcaneus, to give a continuous electrical readout of muscle length.

RESULTS

A total of seven cats was studied. Of these, three cats were implanted with separate force transducers and EMG wires for the MG and SOL muscles in the same hindlimb, four cats were implanted with force transducers and EMG wires for the MG muscle only. One of the latter group was also implanted with a length gauge along the MG muscle. The animals tolerated the
transducers well and were judged to walk normally about 1 wk after implantation. With the final transducer design, the tendons showed no evident damage even after 8 wk of implantation.

**MG and SOL forces during locomotion**

Figures 2, 3, and 4 show records taken from a 2.8-kg cat in which force transducers and EMG wires had been implanted for both the MG and SOL muscles of the left hindlimb. Figure 2 shows the forces produced by these muscles during a slow (left) and a fast (right) walk. The peak force produced by SOL was the same (1.8 kg wt) for the two different treadmill speeds. However, for the slow walk there was a plateau on the falling phase of the force record. A similar profile was found by Manter (22; his Fig. 12) for the calculated ankle torque required during the stance phase and by Grillner (18; his Fig. 5) who converted these torques to expected Achilles tendon force. This plateau was correlated with a prolongation of the electrical activity of the muscle, as can be seen in the traces of integrated EMG. During the slow walk the MG muscle produced, during the peaks, about 40% (0.7 kg wt) of the peak SOL force, whereas during the fast walk this proportion increased to about 80% (1.3 kg wt). Figure 3 illustrates in greater detail two individual step cycles taken from a fast run at 3.0 m/s. The records on the left show a typical step cycle at this speed in which MG produced more peak force (110%, or about 2.0 kg wt) than SOL. The EMG activity in both muscles appeared about 50 ms before foot contact, as described by Engberg and Lundberg (14). Foot contact coincided with an abrupt increase in muscle force. The length changes calculated from joint angles for MG and SOL during the step cycle were somewhat different, since the MG muscle spans both the ankle and knee joints, whereas SOL spans only the ankle. However, the peak forces in both muscles occurred before the end of the yield (E2) phase (the period of increasing muscle length after foot contact). Thus, the magnitude and timing of peak MG and SOL forces are not determined by the onset of muscle shortening.

Figure 3, right, shows an unusual step cycle during the same run, which appeared on the videotape to be an attempt by the cat to convert to a gallop. The swing phase began as usual (left) and at the time of the first extension phase (E2), a brief burst of EMG was seen in the SOL muscle. However, the foot did not extend to contact the

**FIG. 2.** Records from 2.8-kg cat during slow (left set, treadmill speed 0.8 m/s) and fast (right set, speed 1.6 m/s) walking. MG and SOL force records from independent gauges in same leg. MG and SOL electrical activity (EMG) records show raw data (lower trace in each pair) and rectified-integrated traces (above). Integrator (Paynter) filter time constant was 0.05 s; EMG data prefiltered (high pass) at 30 Hz. Arrows at top show footfall (↓) and foot lift (↑) of instrumented left hindlimb from videotape records synchronized to analog tape data (see METHODS).
treadmill, but remained in a flexed position while the contralateral (right) hindlimb continued in contact. During this time another short EMG burst was seen in SOL. The final EMG burst in MG started as usual about 50 ms before left foot contact and there was a large increase in the peak force produced by MG (3.4 kg wt). In contrast, the EMG of SOL was absent prior to foot contact, with a concomitant delay in SOL force production as compared to MG. The muscle lengths during stance in this step were similar to the other steps in the sequence (left records) except that the amount of yield was somewhat greater for both MG and SOL.

The implanted transducers detected virtually no passive force in either MG or SOL during externally imposed movements of knee and ankle through the full physiological range when the animals were under anesthesia. In Fig. 3, when the foot accelerated forward during the swing phase (from the start of each trace to the time of foot touchdown), little passive force was evident in the records from the electrically inactive MG or SOL. Thus, the muscles themselves did not appear to contribute significantly to the passive forces about the ankle joint, which can be quite large near the limits of joint movement in the cat (Fig. 4 in Ref. 18).

**MG and SOL forces during vertical jumping**

Figure 4 illustrates a vertical jump made by the cat from the floor onto a table 120 cm high. Preparation for the jump began with the cat crouching, as indicated by the decreasing ankle and knee angles. During this period the MG and SOL muscles underwent an active lengthening contraction. The force in MG then rose rapidly during the launching phase to a peak of 9.0 kg wt, which was in...
fact greater (15%) than the 7.8 kg wt maximal isometric tetanus developed by the same muscle in the terminal experiment. The EMG activity decreased abruptly about 20 ms prior to liftoff, as found by Zomlefer et al. (34). The peak force developed by SOL during the launching phase of the jump was 1.5 kg wt, which was somewhat less than that developed during locomotion (1.8 kg wt; Figs. 2 and 3). The SOL force decreased before that of MG, probably because of the rapid shortening of SOL, and dropped to zero approximately 40 ms before liftoff despite continued electrical activity in this muscle. Using the videotape records of joint angles, it appeared that the MG muscle length during the launching phase was almost constant until about 30 ms before liftoff. This again reflects the difference between the two-jointed MG muscle and the single-jointed SOL muscle. Since it spans both knee and ankle, the MG length is changed in opposite ways by flexion or extension at either joint. Further, the MG not only contributes its own force to the calcaneus but also can transmit forces generated by the knee extensors by acting as a stiff linkage between femur and calcaneus.

The use of the video system and the trigonometric method for determining muscle length was found to be inadequate for studying jumps since the animal was not as well visualized as during treadmill locomotion. Therefore, one cat was implanted with a length gauge (see METHODS) along the MG muscle, which gave a continuous electrical readout of muscle length, as shown in the lower traces of Fig. 5. In addition, the force transducer used in this cat was linear up to nearly 12 kg wt. Figure 5 shows the results for this cat jumping onto a table at three different heights. The MG muscle underwent active lengthening during the launching phase of all jumps but unlike the yield phase of locomotion (Fig. 3), the peak of the force trace coincided with the peak

![Graphs showing muscle force and EMG activity](image_url)
FIG. 6. Records of MG and SOL force and EMG (raw data plus rectified and integrated) from another cat (2.9 kg) during a sequence of movements during preparation for (step), and landing after (land-stand), a vertical jump to a table 70 cm above the floor. Stand portion during quadrupedal standing while eating food reward.

of the length trace (i.e., when the muscle was at its greatest length during the launching phase) for all three jumps. The peak force developed during the highest jump was 8.7 kg wt, which was 10% greater than the maximal isometric tetanus at optimum length for this muscle (7.9 kg wt) during the terminal experiment. The optimum muscle length for the latter corresponded to a muscle length of about +5 mm on the scale used in Fig. 5. The changes in MG length in this cat during jumping were greater than those estimated from videotape records in Fig. 4. Whether this is a true difference between animals or simply represents more accurate estimates with the length gauge is unknown, although the latter seems more likely.

The division of labor between MG and SOL is dramatically illustrated in a sequence of movements taken from yet another cat and shown in Fig. 6. The peak force generated by SOL was virtually the same (about 1.9 kg wt) for all four movements: stepping, jumping, landing, and standing. The MG muscle, on the other hand, demonstrated a wide range of peak force outputs during the same movements, from 300 to 400 g during standing to nearly 8 kg wt in the jump. The traces of integrated EMG show a concomitant difference in the dynamic ranges of the two muscles. The peaks of integrated EMG in SOL were similar for all four activities (although somewhat smaller during standing), whereas those for MG varied over a much wider range.

In order to compare quantitatively the forces produced by MG and SOL for different movements, the plots shown in Fig. 7 were constructed using data from the same animal.

FIG. 7. Plot of SOL (ordinate) versus MG (abscissa) forces during standing, locomotion, and jumping in same cat shown in Figs. 2–4. Postural points (▲) denote instantaneous forces during several periods of apparently steady quadrupedal standing. Points during locomotion and jumping (●) are peak forces in each muscle. The single gallop point was taken from the step cycle illustrated in Fig. 3, right.
FIG. 8. Mean values of MG and SOL force and rectified-filtered EMG during full output range of hindlimb movements. Postural points during quadrupedal standing averaged for over 40 measurements; jump averaged for five jumps to 120 cm. Points during locomotion averaged from 20 to 65 step cycles. Same cat as used for Fig. 7 but different set of data points. Integrated EMG means plotted on arbitrary linear scale matched to show correspondence between mean force and EMG during locomotion. Note, however, divergence between EMG and force means during standing and jumping. For these measurements, EMG records were rectified and low pass (RC) filtered at 20 Hz (Krohn-Hite filter, model 3322R).

The division of labor between these two muscles is summarized by Fig. 8 in which the mean peak force developed by each muscle (solid symbols, continuous lines) and the associated peak of integrated EMG records (open symbols, dashed lines) are plotted for a variety of activities arranged in order of increasing effort (from standing to jumping). These data show that, overall, the mean peak force output and the mean values for peaks of integrated EMG from the SOL muscle hardly change as locomotion speed increases from slow walk to fast run. Both indexes of activity in MG, however, change over a twofold range during locomotion at increasing speeds. Clearly, the SOL contributes the major fraction of force during quasi-isometric standing although, on the average, its force production and integrated EMG are not as large as during locomotion. It is useful to note that although peak SOL force changes little as locomotion speed increases, nevertheless the SOL muscle produces more peak force than MG, up to fast speeds of running (3 m/s). Although there is relatively good correspondence between the average force and integrated EMG values, it cannot be concluded that integrated EMG records accurately predict force production because the relation between instantaneous (and even peak) EMG and force was highly variable (see, e.g., Figs. 2 and 6). Clearly, a detailed correlation between EMG and force developed by a muscle must also take account of length changes occurring in that muscle.

DISCUSSION

The present results demonstrate that when the forces from two contrasting triceps heads are individually measured, there is a distinct difference in the division of labor between the slow-twitch SOL and the mixed (nominally “fast twitch”) MG. Quadrupedal standing can at times result in as much SOL force (up to 1.8 kg wt in a 3-kg cat) as that muscle produces under any force output during jumping probably reflects the rapid shortening of this single-joint muscle at a time when the MG is either virtually isometric (see Fig. 4) or still lengthening (Fig. 5) due to its origin above the knee.
conditions, while the MG typically produces only a few hundred grams during quiet standing (Figs. 6, 7, and 8). Progressively increasing speeds of locomotion require concomitantly greater total ankle extensor forces, and this is evidently supplied by MG as well as by the lateral gastrocnemius (LG), with some possible contribution also from the plantaris (see Refs. 17, 31). The ‘‘fast’’ triceps heads, MG and LG, are both mixed muscles composed of similar motor unit populations (as judged by both physiological and histochemical studies; Ref. 8), and they presumably act similarly during locomotion and jumping. The observed range of MG force output modulation, from quadrupedal standing to maximum vertical jumping, is greater than 10 fold. The LG dynamic range is presumably similar. In contrast, for the same range of movements, average force output of SOL varies only over a less than twofold range.

In an unpublished thesis, Yager (32) described measurement of forces produced by the combined ankle extensor muscles in the cat using an implanted belt-buckle transducer placed on the whole Achilles tendon (see also Refs. 2, 28). He found that the forces recorded from the Achilles tendon during stepping were more or less linearly related to the EMG activity recorded over the surface of the triceps surae muscles, but made no attempt to record force production from individual heads of the triceps surae and no absolute force data were reported.

The present observations on the contrasting force output patterns of MG and SOL are entirely in accord with recent EMG studies of Smith and co workers (29), who examined quantitative electrical activity in SOL and LG during a wide range of movements in unrestrained cats. In that study, the EMG records from LG were obtained from the lateral edge of the muscle where the muscle fiber population contained a higher percentage (90%) of type FG fibers (typical of motor units with large force output, rapid fatigue and, probably, high functional threshold, the type FF units; see Ref. 8) than that of the LG muscle as a whole (66% FG fibers; Ref. 1). This apparent bias in the EMG results probably accounts for the wider (fourfold) range in peak LG EMG found by Smith et al. (29) for locomotion between 0.5 and 3.0 m/s, as compared to the present range (threefold) over the same speeds (Fig. 8). Smith et al. (29) found a narrow (<1.5-fold) range of average SOL EMG modulation from standing to jumping, as was true in the present study (Fig. 8).

Records of rectified and integrated EMG represent some function of muscle fiber activation and have been used (e.g., Ref. 29) to infer variations in muscle force output. The relation between EMG and force output may be reasonably linear over a restricted range of movements (e.g., treadmill walking at various speeds, Fig. 8; see also Ref. 32), but there is considerable scatter for individual measurements. The methods for EMG signal processing are not standardized and the signal itself depends on electrode configuration and on the characteristics of the local population of muscle fibers ‘‘seen’’ by the electrode, which may or may not be representative of the overall fiber population in the muscle of interest. Finally, the EMG alone provides no reference points for estimating absolute force. For all these reasons, direct force measurements from individual muscles seem advantageous for making inferences about muscle and motor pool usage during normal movement. However, the interpretation of the force records is also not simple.

At a given muscle length, active muscle force is graded by recruitment and derecruitment of motor units and modulation of firing frequency of the active units. The well-known dependence of muscle force on isometric length is also important in the interpretation of records during postural (i.e., quasi-isometric) actions, and this effect may play a considerable role in modulating SOL forces over the range of observed ankle angles (Fig. 3 of Ref. 27; see also Ref. 18).

However, in interpreting the forces developed during dynamic movements such as walking, running, and jumping, care must be taken in drawing conclusions based on the isometric force-length relationship for particular muscles. The force records obtained during walking and running indicate that the peak MG and SOL forces occur during the yield (E2) phase of the step cycle when the muscles are still lengthening (16). It is known that active lengthening may produce marked enhancement of force output from muscles (e.g., Ref. 11), but this
effect (at least in the cat SOL) is also dependent on activation frequency (20). Even if the muscle is operating over a length range equivalent to the relatively flat portion of the isometric tetanus force-length curve (30), stretch of the active muscle, such as occurs during the yield phase of the walk, may produce a large increase in force over the isometric level (see, e.g., Fig. 10 of Ref. 25).

**SOL forces during standing and locomotion**

The present results show that the SOL muscle can generate as much as 1.8 kg of force during quasi-isometric standing (e.g., Fig. 6), whereas the same muscle produced, in maximum fused tetanic contraction, 2.8 kg wt at optimum length (100/s stimulus rate). When driven by synaptic inputs, SOL motoneurons in the cat probably fire at relatively low frequencies (19) and the isometric force output from each SOL motor unit would probably be no more than about 75% of maximum (at optimum length; see Ref. 9), or about 2.1 kg wt for 100% recruitment. Given the fact that the isometric optimum length of the cat SOL muscle occurs at ankle angles around 60° for tetani (at 10–30/s stimulation; Ref. 26), and greater angles (corresponding to shorter SOL lengths) are observed during standing, 100% recruitment should produce less than 2 kg wt. Thus, quiet standing in the cat probably requires, on some occasions at least, recruitment of the entire SOL motor-unit population, with each unit firing near its maximum physiological frequency. Even though the average SOL forces recorded during standing are lower (approximately 1.0 kg wt; Fig. 8), these may also at times involve near-complete recruitment of the SOL motor-unit pool, given the steep isometric force-length relationship for this muscle at ankle angles around 90° (18, 27). It should be noted, however, that SOL forces are quite small in some examples of standing (Fig. 7), so that postural actions clearly do not always involve complete SOL recruitment. It is also interesting in this regard that there is a certain degree of independence between SOL and MG action in standing (Fig. 7).

For reasons mentioned in the preceding section, interpretation of the SOL forces produced during treadmill locomotion at various speeds is complicated. Stepping requires motor-unit firing in relatively short bursts, precisely timed with respect to foot fall. During a run at 3.0 m/s (Fig. 3), SOL force reached a peak approximately 40 ms after foot contact, and returned to baseline less than 100 ms later. EMG activity in SOL could be detected 50 ms before foot contact and lasted throughout the period of force production. For comparison, the average single twitch time to peak for SOL motor units is approximately 80–90 ms with the muscle isometric (7, 23).

Since SOL muscle units contract relatively slowly, the time at which a unit begins firing with respect to foot contact will determine the contribution that that unit can make to the peak of SOL force. Even allowing for the effect of active lengthening, it would appear that those SOL units that begin firing before foot contact should contribute relatively more to the peak of SOL force than those that fire after foot contact, at least during fast runs. This timing effect may be less critical during slow walks where the force lasts over several hundred milliseconds (Fig. 2). The mechanical stiffness of the active SOL motor units during the yield phase, when the muscle is being stretched, is probably responsible for the rapid rise of the SOL force during the yield phase of the run (e.g., see Ref. 18). This conclusion is further supported by the fact that the rate of rise of SOL force is much greater during fast treadmill locomotion than during slow walks (see Figs. 2 and 3), presumably because the rate and extent of muscle lengthening during the yield are also much greater during fast runs as compared to slow walks (16).

It seems paradoxical that the average peak SOL force was found to be the same over the whole range of treadmill locomotion studied (0.6–3.0 m/s), in view of the greater rate and extent of stretch during fast as compared to slow locomotion. However, as discussed above, the period of force production is so brief during fast runs that it may not allow all of the recruited SOL units to contribute fully to the peak of SOL force. The data obtained in the present study suggest that this negative effect balances to some extent the force enhancement due to increased active lengthening in the faster runs, resulting in an apparent "saturation" of peak SOL force irrespective of locomotion speed.
The presumed full recruitment of SOL motor units at relatively low levels of output demand fits well with its motor-unit composition. The cat SOL is made up entirely of type S, slow-twitch motor units with a rather narrow range of properties (7, 23). SOL motoneurons are all powerfully excited by primary, or group Ia, muscle spindle afferents (3, 13) and, if one accepts the view (10) that the strength of group Ia synaptic connectivity is a reasonable index of susceptibility to recruitment (as it is in the stretch reflex (4, 12)), then the evident readiness of SOL recruitment and the limited dynamic range over which it is modulated are not surprising.

Correlation of dynamic range with motor-unit properties in MG

Recently, Burke, Rymer, and Walsh (10) showed that the strength of group Ia connectivity to MG motoneurons is closely related to motor unit type. The average amplitude of MG Ia EPSPs was greatest in motoneurons of the slowly contracting, fatigue-resistant type S units, somewhat less in the faster contracting but fatigue-resistant type FR and F(int) units, and least among the large force, fast-twitch but fatigue-sensitive type FF units. Based on the assumption that the strength of group Ia input, and of other functionally relevant input systems similarly organized, is the key factor that governs MG motor-unit recruitment order (see Ref. 5 for a discussion of this issue), a recruitment model of the MG motor-unit pool was constructed (Fig. 8 of Ref. 10). The estimates made for absolute force outputs from the cat MG during locomotion, which were based on the fragmentary indirect evidence then available, have been essentially corroborated by the present results.

The use of group Ia EPSP amplitude as a "recruitment rule" for the cat MG pool suggests that MG motor units are recruited in the following general sequence: type S → type FR → type F(int) → type FF. We have reexamined the estimated force production from MG motor units, now using this sequence as the recruitment rule rather than Ia EPSP amplitude. For purposes of argument we will assume that all type S units are recruited fully before any type FR unit, and so on through the MG unit pool. The curve in Fig. 9 shows the cumulative force (in percent of total; left ordinate) developed at the MG tendon if: 1) recruitment of the MG motor-unit pool occurs according to the above recruitment rule, 2) the first unit recruited produces its maximum isometric tetanic force before the next unit becomes active, and 3) each subsequent unit adds its full tetanic force linearly to that of the already active units.

The nonlinear character of the relation between percent cumulative force output (left ordinate) and percent of the motor unit pool recruited (abscissa) is due to the strong negative correlation between average force output per unit and motor-unit type (8; see also Fig. 3 of Ref. 10).

The above set of assumptions is oversimplified in that recruitment is almost certainly not so strictly tied to the unit-type groups. Furthermore, motor units when recruited probably exhibit some range of firing-frequency modulation as other units become active, as occurs in human forearm muscles (see Refs. 15, 24). Mitigating such
objections is the fact that considerable indirect evidence suggests that the general order of motor-unit recruitment is in fact related closely, if not precisely, to both motor-unit type and to unit force output in the pattern assumed for the present model (for references, see Ref. 6). MG motor units can produce forces approaching fused isometric tetanic force, even at low average firing frequencies, if one or more short intervals (‘doublets’) occur as they are activated (9). Doublet firing has been found to occur in a large proportion of motor units active during fictive locomotion in mesencephalic cat preparations (33). The active lengthening of MG during the step cycle presumably enhances force output from MG motor units as it appears to do in SOL. The effects of doublet firing and of active lengthening during locomotion both tend to increase motor-unit forces above those expected for a given rate of motoneuron firing under isometric conditions. In the absence of quantitative data with which to construct a more accurate model, we suggest that the curve shown in Fig. 9, although based on isometric force data, nevertheless represents a reasonable first estimate of the recruitment-force output relation characteristic of the MG motor-unit population during locomotion.

The right-hand ordinate of Fig. 9, scaled in absolute force, is based on data from a 2.8-kg cat in which fused isometric tetanus of the MG muscle (100% recruitment) produced 8 kg wt of force. The open circles and brackets show the means and standard deviations of MG forces measured in the same cat during standing, locomotion at four different treadmill speeds, and during 120-cm vertical jumps. Extrapolating these forces onto the curve of force versus recruitment suggests that quadrupedal standing in the cat may involve, primarily if not exclusively, activation of the type S motor-unit complement. The model further suggests that the increasing output from MG during locomotion must involve recruitment of the fatigue-resistant fast-twitch (type FR) units. However, it is surprising that even fast runs (at 3 m/s) may require predominant recruitment of only that half of the MG motor unit pool that is fatigue resistant (summing the outputs of S, FR, and F(int) units together). On the average, even fast running demands less than 25% of the maximum isometric force capability of the MG muscle.

The MG forces developed during vertical jumps to about 120 cm are very close to those produced by the fully tetanized isometric MG muscle. If we make allowance for the competing effects of less-than-fused firing frequency versus doublet firing and active lengthening, the correspondence between the observed jump forces and the estimated forces generated by 100% MG recruitment suggests that the MG motor-unit pool is essentially fully recruited during the intense burst that occurs during such jumps (Figs. 5 and 6). The fact that some vertical jumps involve forces greater (by 10–15%) than maximum fused tetani can be accounted for by the factor of active lengthening during the launch phase and by the fact that the fully active MG muscle must possess great inherent stiffness enabling it, by virtue of its two-joint disposition, to transmit forces from the powerful knee extensors to the calcaneus. The present results, together with previous evidence, suggest that the type FF units, which represent about 45% of the MG motor-unit pool and which produce about 75% of its total force output, may be largely unused even during rather fast running. They are, however, essential for brief but very large force demands such as occur, presumably, in galloping and which certainly occur in vertical jumps. The relative infrequency of such demands during the normal activities of cats fits very well with the extreme susceptibility of the type FF units to mechanical fatigue during even modest levels of repetitive activity (8).

The contrasting terms tonic and phasic are sometimes used to describe the supposed functional characteristics of slow-twitch versus fast-twitch muscles, motor units, and even motoneurons. The present results show, however, that the nominally tonic SOL can produce as much or more peak force during locomotion as the MG, and the rates of rise in SOL and MG forces during stance are also comparable despite their very different motor-unit populations. The observations can only be explained by taking account of the effect of active
lengthening in addition to factors of motor-unit properties and activity patterns. The SOL also clearly acts phasically during vertical jumping. The adjectives tonic and phasic cannot really describe the range of action of either SOL or MG, and it may be best to abandon these terms as descriptors of muscles or their motor units.

REFERENCES


