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Cat Hindlimb Motoneurons During Locomotion. III. Functional Segregation in Sartorius

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SUMMARY AND CONCLUSIONS

1. Cat sartorius has two distinct anatomical portions, anterior (SA-a) and medial (SA-m). SA-a acts to extend the knee and also to flex the hip. SA-m acts to flex both the knee and the hip. The objective of this study was to investigate how a "single motoneuron pool" is used to control at least three separate functions mediated by the two anatomical portions of one muscle.

2. Discharge patterns of single motoneurons projecting to the sartorius muscle were recorded using floating microelectrodes implanted in the L_5 ventral root of cats. The electromyographic activity generated by the anterior and medial portions of sartorius was recorded with chronically implanted electrodes. The muscle portion innervated by each motoneuron was determined by spike-triggered averaging of the EMGs during walking on a motorized treadmill.

3. During normal locomotion, SA-a exhibited two bursts of EMG activity per step cycle, one during the stance phase and one during the late swing phase. In contrast, every recorded motoneuron projecting to SA-a discharged a single burst of action potentials per step cycle. Some SA-a motoneurons discharged only during the stance phase, whereas other motoneurons discharged only during the late swing phase. In all cases, the instantaneous frequencygram of the motoneuron was well fit by the rectified smoothed EMG envelope generated by SA-a during the appropriate phase of the step cycle.

4. During normal locomotion, SA-m exhibited a single burst of EMG activity per step cycle, during the swing phase. The temporal characteristics of the EMG bursts recorded from SA-m differed from the swing-phase EMG bursts generated by SA-a. The SA-m EMG bursts typically began earlier and peaked earlier than the swing-phase SA-a EMG bursts. Activity in SA-m declined progressively during the E_1 phase of swing, whereas activity during swing in SA-a peaked late in the E_1 phase and shut off abruptly before footfall.

5. Each sartorius motoneuron active during swing had an instantaneous frequencygram that fell into one of two classes: a group whose discharge profiles were best fit by the SA-a EMG profile and a group whose frequencygrams were best fit by the SA-m EMG profile.

6. We conclude that the motoneuron pool that innervates the cat sartorius muscle consists of three functionally separate motoneuron groups, each of which is independently recruited to perform one of three tasks: knee extension (stance phase), knee and hip flexion (early swing phase), or knee extension and hip flexion (late swing phase).

7. These distinctions are correlated with heterogeneities in both skeletal action (SA-a vs. SA-m) and kinematic function (SA-a actively shortens during swing and actively lengthens during stance). The existence of such functional distinctions suggests circumstances for which the traditional concepts of "one muscle-one motoneuron pool" and orderly recruitment by size of the motoneurons comprising a motor nucleus may require modification.

INTRODUCTION

The traditional concept of a "motor pool" includes all the motoneurons that innervate

one muscle. It is the physiological equivalent of the anatomically defined "motor nucleus." The motoneurons in a pool are generally believed to share the same sources of synaptic input (6), to be controlled by a common drive (12), and to be progressively recruited in a fixed order correlated with cell size (7). The premise of "one muscle-one motoneuron pool" and a control hypothesis based on orderly recruitment within a pool have been supported for anatomically simple muscles acting across a single joint (1, 8, 9).

The anatomical design and physiological control of sartorius, a biarticular muscle in the anterior thigh, is difficult to understand based on the action of a single motoneuron pool as defined above. By virtue of its distributed insertion, cat sartorius has two distinct anatomical actions (Fig. 1*A*). The anterior part (SA-a) inserts on the proximal patella, whereas the medial part (SA-m) inserts along the patellar ligament and the medial edge of the tibia. Thus SA-a extends the knee, whereas SA-m flexes the knee. By virtue of their common origin on the anterior iliac crest, both portions are anatomically designed to flex the hip. This allows sartorius to contribute to three skeletal actions: hip flexion, knee extension, and knee flexion. This paper describes when these actions occur during walking, what muscle portion contributes to them, and how the individual motoneurons comprising this motor pool are functionally organized to perform these tasks. Preliminary reports have been published (10, 13).

METHODS

Recording devices

In this study we used implanted electrodes and transducers described in companion papers (8, 12) to record EMG, muscle length and force, and the activity of single motoneurons projecting to sartorius, in unrestrained cats trained to walk on a motorized treadmill. Briefly, the activity of single motoneurons was recorded extracellularly using floating "hatpin" microelectrodes implanted in the L_5 ventral root. The axonal conduction velocity (CV) and the muscle of destination of each motoneuron were determined, respectively, by spike-triggered averaging of records from cuff electrodes implanted on the femoral nerve and from EMG electrodes implanted in SA-a, SA-m, and in each head of

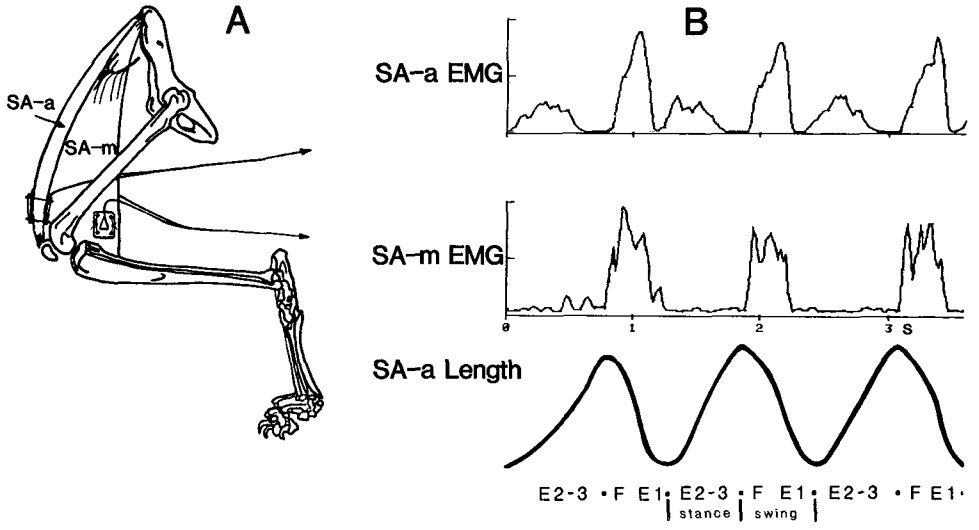

FIG. 1. *A*: the anterior (SA-a) and medial (SA-m) parts of sartorius and the locations of the EMG "sandwich" electrodes are shown schematically. A saline-filled length gauge (not shown) spanned from a bone screw on the iliac crest to the patella. Further description of implanted devices is found in Refs. 8 and 12. *B*: examples of muscle length and EMG activity recorded during walking. The four stages of the Phillipson step cycle are indicated (F = knee flexion; E_1, E_2, E_3 = stages of extension). EMG records were rectified, sampled in 4-ms bins, integrated, and digitally filtered. SA-a was active twice per step, SA-m only once. During the step cycle the length of SA-a (*bottom trace*) changed from ~11 cm (bottom of excursion; end of E_1) to ~15 cm (top of excursion; end of E_3).

quadriceps (8). For each portion of sartorius we used a "sandwich" pair of EMG electrodes, consisting of two 10 × 10 mm patches of Silastic film (Dow Corning 500-3). A multistrand stainless steel wire electrode was sewn onto the inside surface of each patch (Bergen Wire). Electrode lead wires were insulated except for the exposed recording areas. A diagram of this electrode design was shown in Fig. 2*D* of Ref. 8. Sandwich EMG electrodes encompassed within insulating walls a discrete portion of the muscle. Since the flow of action currents was confined mainly to those generated by nearby sources, the electrical activity generated locally was recorded cleanly with little contamination from other sources. Fortuitously, the activity patterns of SA-m single units were discriminated from sandwich EMG electrode records on two occasions and included in this sample.

Data analysis

The instantaneous frequencygrams of stance-phase motoneurons that were identified as projecting to sartorius were computer fit to the smoothed digitally filtered EMG profile of each anterior thigh muscle (see Ref. 12 for detailed description). For swing-phase sartorius motoneurons, the frequencygram was fit to both the SA-a and the SA-m EMG profiles. The fraction of the variance in motoneuron firing frequency that was accounted for by the EMG of each head of sartorius was taken as further indication of the portion of the muscle where the muscle unit resided. The identity of each motoneu-

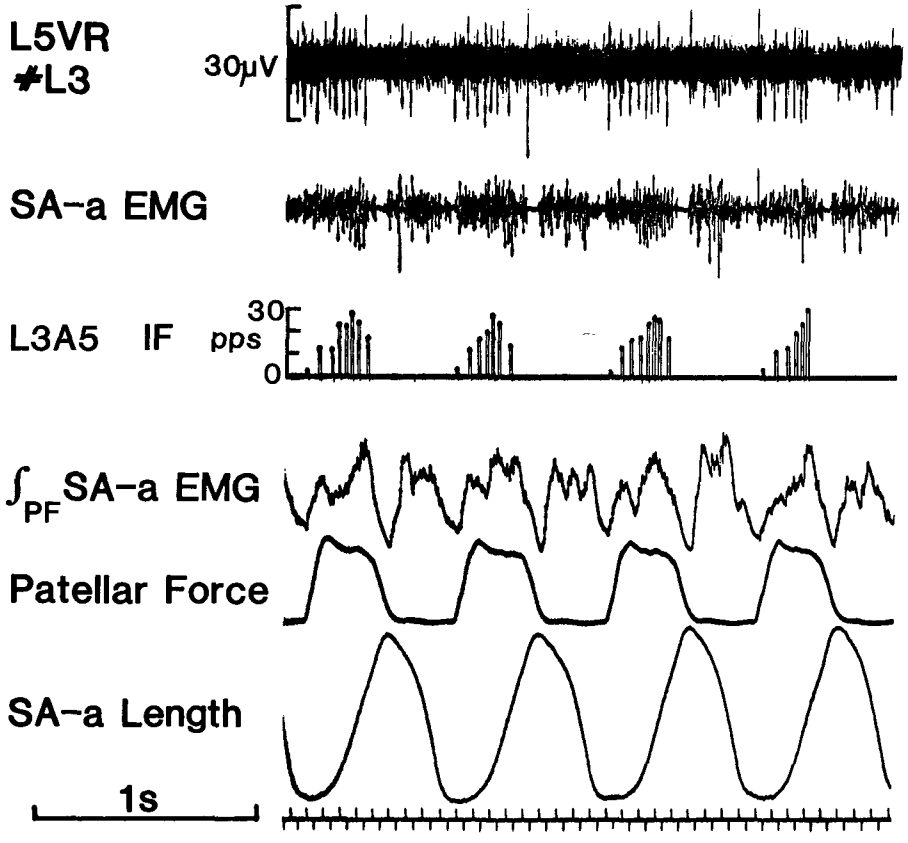

FIG. 2. Discharge patterns of a sartorius motoneuron (L3A5) active during the stance phase of walking. *Traces from top*: the raw record obtained from microelectrode no. 3 in *cat L*, dominated by spikes generated by motoneuron L3A5; raw SA-a EMG; instantaneous frequency (IF) of motoneuron L3A5; Paynter-filtered (PF) EMG of SA-a (8); force recorded from patellar ligament; length of SA-a; and treadmill motion (*upgoing vertical marks* were spaced every 5 cm on moving belt). Treadmill speed was 0.67 m/s. Note that motoneuron L3A5 only fired during the stance phase (high values of patellar force), whereas SA-a showed 2 EMG bursts per step cycle, during stance and during swing. Note also that the SA-a EMG amplitude during swing exceeded the threshold for recruitment of unit L3A5 (8, 12) and sometimes exceeded the amplitude of stance-phase EMG bursts.

ron was thus based on both anatomical and functional relationships. The threshold of recruitment, T(0.5), of each motoneuron was computed with respect to the target muscle EMG at an interpolated treadmill speed of 0.5 m/s (8, 12).

RESULTS

Two major features differentiated the electromyographic activity recorded from the two portions of sartorius. First, SA-a exhibited two distinct bursts of EMG activity per step cycle, one during the stance phase and the other during the swing phase (see also Ref. 4), whereas SA-m exhibited only one burst of activity, during the swing phase. Second, the shape of the SA-m EMG burst differed from the EMG burst recorded from SA-a during swing. The SA-m burst peaked early in the flexion phase (F) and declined gradually during the first extension phase (E_1). The swing burst in SA-a developed slowly, peaked late in the E_1 phase, and ended abruptly. Examples of EMG records obtained during locomotion are shown in Fig. 1*B*. SA-a length records, obtained from a saline-filled gauge attached proximally to the iliac crest and distally to fascia above the patella, are also shown in Fig. 1*B*. The length gauge, since it paralleled the biarticular course of SA-a, had a larger lever arm about the hip joint than about the knee joint and thus it reflected mainly hip movement.

Every one of the 13 motoneurons innervating sartorius invariably was found to discharge a single burst of spikes per step, either during stance or during swing, in contrast to the double-burst EMG pattern characteristic of the anterior muscle portion as a whole. Examples are shown in Figs. 2 and 3. Figure 2 shows a motoneuron active exclusively during stance [L3A5, CV = 121 m/s, T(0.5) = 37%]. Figure 3 shows a motoneuron active only during swing [G3A6, CV = 104 m/s, T(0.5) = 50%]. Of the 13 motoneurons identified as innervating sartorius, nine were active only during the swing phase, whereas the other four discharged only during the stance phase. The finding that sartorius motoneurons fired a single burst per step held true for the entire range of treadmill speeds tested (0.13–1.25 m/s).

A further partition among the nine sartorius

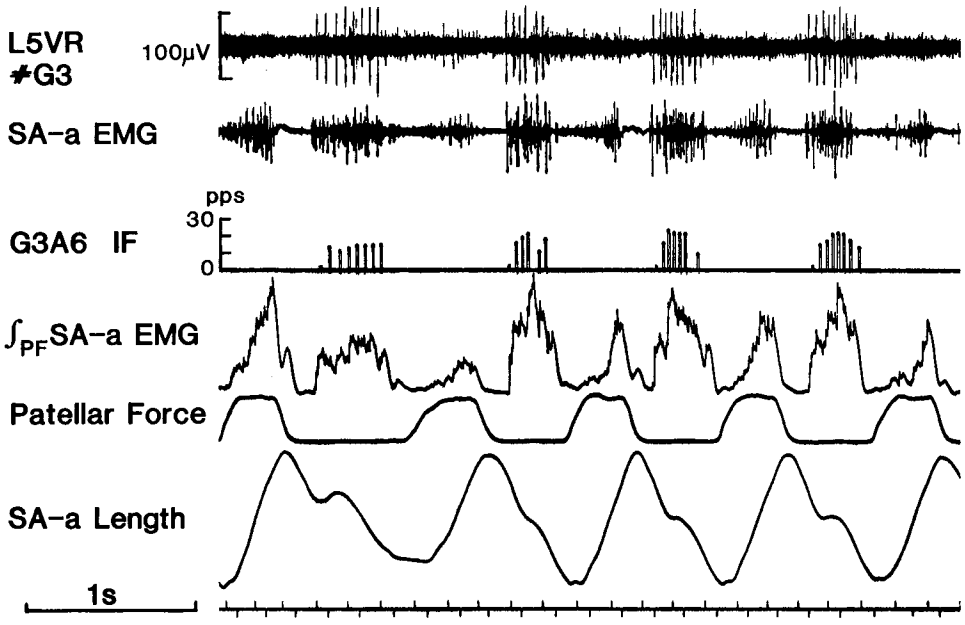

FIG. 3. Discharge patterns of a sartorius motoneuron (G3A6) active during the swing phase of walking. *Traces* as in Fig. 2. Treadmill speed was 0.27 m/s. Unit G3A6 was only active during swing (low values of patellar force). The inflexion seen in the SA-a length trace during midswing was caused by a characteristic hesitation in this cat's natural gait.

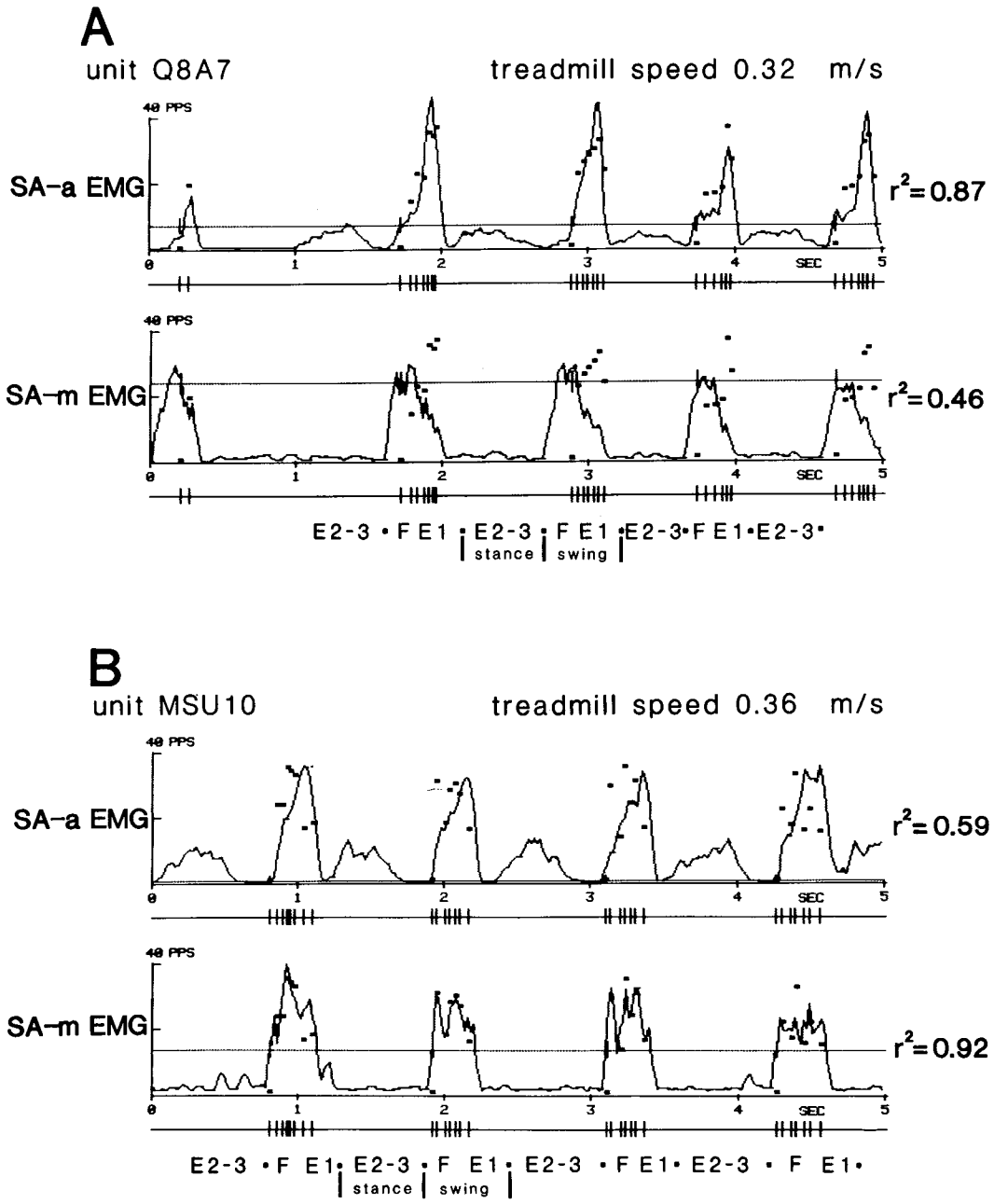

FIG. 4. Examples of partition of sartorius motoneurons active during swing phase into "F-phase task" and "E_1-phase task" groups. The displays of the SA-a and SA-m EMG profiles were scaled for best fit to the frequencygrams of two swing-phase sartorius motoneurons, shown superimposed. Variance values shown on *right* (r^2) were computed for 16 s of data at constant-speed walking that included the 5 s of data shown (see 12 for further description). *A*: discharge patterns of an "E_1-phase task" sartorius motoneuron recorded during walking. The instantaneous frequency of unit Q8A7 was well correlated with the SA-a EMG profile (r^2 = 0.87) and poorly correlated with the SA-m EMG profile (r^2 = 0.46). *B*: discharge patterns of a "F-phase task" sartorius motor unit recorded during walking. Unit MSU10 was better correlated with the SA-m EMG profile (r^2 = 0.92) than the SA-a EMG (r^2 = 0.59). For both units, the difference in the quality of fit by the two muscle portions was significant at the 1% confidence level (see Table 1).

motoneurons active during swing became apparent when we applied the computer-fitting approach described in the previous paper (12). The frequencygrams of individual swing-phase motoneurons typically resembled the swing-phase EMG profile of one part of the muscle more closely than the other part. Computation of the correlation between single-unit discharge profiles and the SA-a or SA-m EMG profiles demonstrated that the difference was often significant, as shown in Table 1. Examples of two such units are shown in Fig. 4, *A* and *B*. The discharge profile of the swing-phase motoneuron in Fig. 4*A* was strongly correlated with the SA-a EMG burst profile but weakly correlated with the SA-m EMG profile. This unit was classified as an "E_1-phase task" motoneuron. Conversely, the frequencygram for the unit shown in Fig. 4*B* was best correlated with the SA-m EMG profile and the unit was classified as an "F-phase task" unit. Two separate populations of swing-phase motoneurons could thus be identified in sartorius.

TABLE 1. *Identification of sartorius motoneurons active during swing*

Unit	Correlation coefficient (r)		STA Motor-unit Potential, μV	
	SA-a	SA-m	SA-a	SA-m
G3A6	0.95	NA	255	NA
L4A14	0.96	0.95	68	46
L2A42	0.925	0.915	56*	18
M10B3	0.94	0.915	69*	13
MSU3	0.79	0.89†	NA	NA
M10A10	0.98†	0.93	85*	8
MSU10 (doublets deleted)	0.81	0.93†	NA	NA
Q8A7	0.89†	0.75	75*	46
Q10A37	0.93†	0.82	78*	10

STA, spike-triggered averaged. *Motor-unit potential discrimination assigned to SA-a. † Difference significant at the 1% level.

Table 1 summarizes our findings for nine sartorius motoneurons active during swing. *Cat G* was done early in the series, before we started installing separate EMG recording electrodes in SA-m. Therefore, a comparison between the fits provided by the SA-a and SA-m EMG profiles was not possible for unit G3A6. Of the remaining eight sartorius motoneurons that were activated during swing, five had significantly different correlation coefficients, *r*, when we fitted their frequencygrams to the EMG profiles of SA-a and SA-m (Table 1, last 5 units). For three of these five units, the results of spike-triggered averaging were clearly different in the two muscle portions, although a measure of significance was not available. The results of spike-triggered averaging coincided with the result of the fits. The other two units (MSU3 and MSU10) were discriminated directly from the SA-m electromyogram, so spike-triggered averaging was not possible. However, the location of the muscle unit within SA-m was certain.

For two other units (L2A42, M10B3) the amplitudes of the muscle unit potentials obtained by spike-triggered averaging from the two SA heads differed by more than a factor of 3, suggesting that the muscle unit was localized within SA-a in both cases (8). SA-a also gave better fits, although the differences were not significant. The final unit, L4A14, also appeared to innervate SA-a by both methods, but the difference in correlation coefficient was again not significant. Interestingly, postmortem inspection revealed that, in *cat L*, the electrodes making up the SA-a "sandwich" had become detached and one had migrated medially, making it likely that the SA-a EMG records were contaminated with SA-m activity. This may have accounted for the comparable correlation coefficient values rendered by the two recorded EMGs.

In general, because of the extended shape of the SA-m muscle and the fairly localized territories of single motor units, the amplitude of spike-triggered averaged records from SA-m may have depended on the exact location of the SA-m electrodes in each cat preparation. This may have accounted for the unusual ability of the large surface area low-impedance "sandwich" EMG electrodes to record clearly separable single-unit action potentials from SA-m in at least two occasions (units MSU3 and MSU10). It should be noted that in *cat M*, the SA-m EMG electrodes were placed at the extreme distal and medial corner of the muscle, whereas in other cats the location was more central on the medial belly of the muscle.

DISCUSSION

The main conclusion from this study is that the cat sartorius motor pool is composed of at

least three functional groups of motoneurons. Each group is independently recruited during a different phase of locomotion to perform one of three kinematic tasks. *1*) F phase task: SA-m provides forces needed to flex both the hip and the knee in the early part of the swing phase. This task is characterized by rapid active shortening of SA-m as a result of motion at both the hip and knee. *2*) E_1 phase task: SA-a provides forces needed to complete hip flexion and extend the knee in the late part of the swing phase. This task is characterized by rapid active shortening of SA-a as a result of motion at both the hip and the knee. *3*) E_{2-3} phase task: SA-a provides forces needed to extend the knee during the stance phase. In late stance (E_3), when the knee is significantly extended, the monarticular knee extensors (vasti) must operate under the disadvantageous conditions of suboptimal fiber length and high shortening velocity. In contrast, since SA-a and also RF have large lever arms about the hip joint and the hip is being extended, these biarticular muscles are actually lengthening throughout the stance phase, making them efficient generators of knee extensor torque.

The motor units responsible for the second and third tasks appear to be co-extensive throughout SA-a, as is shown schematically in Fig. 5, whereas the first group innervates only SA-m. Retrograde labeling of the sartorius motor nucleus by HRP has confirmed that all motoneurons projecting to the muscle form a single contiguous nucleus in the ventral horn (16). Almost 30 years ago, Eccles and Lundberg (3) suggested the existence of two functional groups within the sartorius motoneuron pool, on the basis of Ia synaptic projections

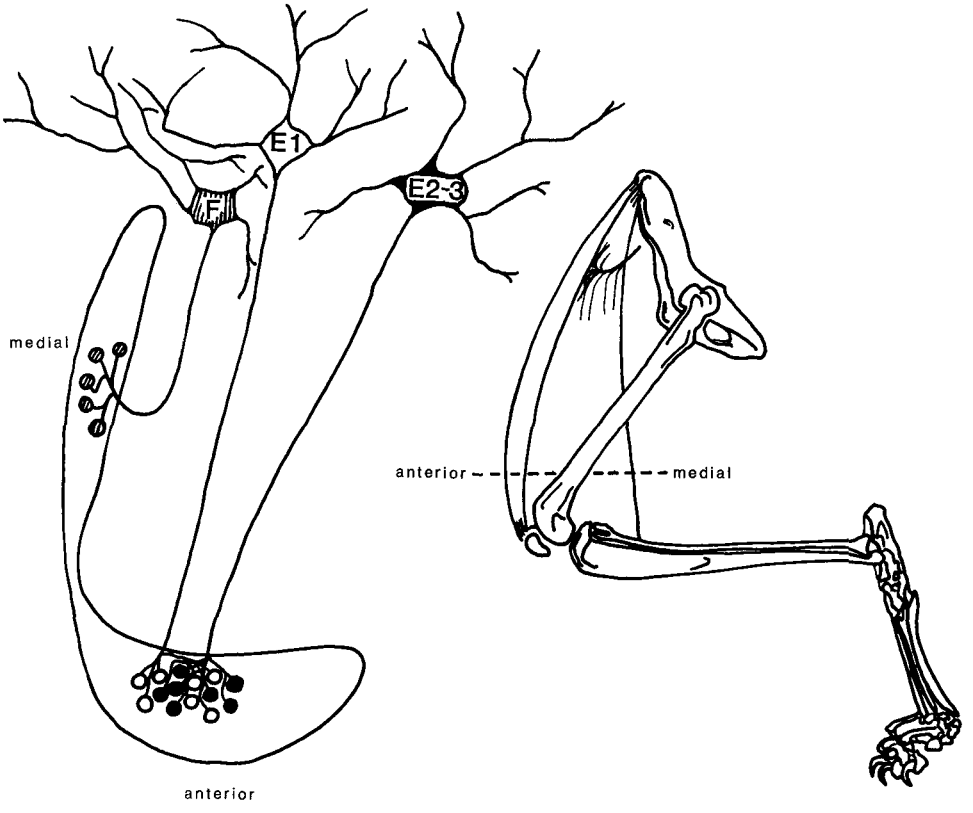

FIG. 5. Schematic diagram showing the anatomical and functional segregation of sartorius motoneurons into three independently recruitable populations. *Left diagram* shows a transverse section of the muscle at the level indicated by the *dashed line* in the *right diagram*. The SA-a portion ("anterior") is only innervated by E_1-task and E_{2-3} task motoneurons whose motor unit territories are probably intermingled. The SA-m portion ("medial") is innervated exclusively by F-task motoneurons. The cell bodies form a single contiguous motor nucleus in the ventral horn.

observed in anesthetized cats. In the absence of data on recruitment patterns of sartorius motoneurons during movements, they assumed that the two groups would be correlated with the two anatomical divisions of the muscle, anterior and medial, which have different mechanical action on the knee. We suggest here that the number of functional groups is at least three, and that two functionally different groups co-exist within *a single* anatomical subdivision, SA-a, where the mechanical action is uniform.

The assignment of specific roles to separate populations of motoneurons is a solution to the problem of how to control several functions in a single muscle while also retaining most of the central organizational properties of motoneuron pools. In addition, the division of tasks among motor units recruited at different times during the step cycle may reflect another important functional advantage. For SA-a, the mechanical demands differ markedly for muscle units of each population. Units active during the swing phase (F or E_1) shorten rapidly while active. In contrast, units active during stance undergo considerable lengthening during the yield phase of stance (E_2; see length gauge records in Figs. 1–3). The specialization of cat SA-a motor units into populations that either shorten or lengthen when active suggests that design differences may also exist in the contractile apparatus of the muscle fibers.

In agreement with our finding for normal cat locomotion, intracellular records during "fictive" cat locomotion have also demonstrated just one period of membrane depolarization and one burst of spike activity per step cycle for sartorius motoneurons (15; also S. J. Shefchyk and L. M. Jordan, personal communication). This is in contrast to semitendinosus motoneurons, which depolarize twice and fire two bursts per step cycle in "fictive" locomotion (15). Interestingly, semitendinosus differs from SA-a in that both periods of EMG activity coincide with similar patterns of motion of the muscle (14). The observed difference in activation patterns of motoneurons innervating sartorius and semitendinosus, both biarticular muscles acting at hip and knee, may be related to the different kinematic situation in the two cases (14).

Our findings for cat sartorius may have wider generality. Many mammalian limb muscles can actually perform multiple functions either because they pull in more than one direction or because they span more than one joint. For example, the first dorsal interosseus muscle in the human hand acts to abduct and also to flex the index finger. The progressive recruitment of motoneurons in one pool, as defined above, could not possibly mediate abduction and flexion independently. To explain this apparent paradox, it has recently been suggested (2) that interosseus can perform only abduction as a prime mover and that its role in flexion is limited to that of a synergist of the long flexor muscles. The recruitment order of motor units could be shifted somewhat by changing from one motor task to the other (cf. Ref. 5).

Based on our findings in cat sartorius, we propose an alternative possibility for the control of multifunctional muscles, among which the human first dorsal interosseus and perhaps also biceps brachii (17) may be included. In certain cases a muscle might be innervated by several groups of motoneurons, each group having inherently different central connections, recruitment patterns, and perhaps also muscle units with mechanical properties specialized for the performance of a different task. The muscle unit territories could still co-exist intermingled within the muscle. This design would allow for the independent recruitment of these groups of motor units in different task-specific combinations. The simplifying "size principle" apparent in the inputs to and the recruitment of the motor pools of unifunctional muscles could still hold for the motoneurons comprising each group. The traditional concept of "motor pool," which stemmed from purely anatomical considerations, would thus be replaced with the concept of task-specific groups of motoneurons whose properties would be defined on functional, in addition to morphological, criteria.

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