

TELEMETERED ELECTROMYOGRAPHY OF THE FAST AND SLOW EXTENSORS OF THE LEG OF THE BROWN LEMUR (*LEMUR FULVUS*)

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SUMMARY

Quantitative telemetered electromyography from the four heads of the quadriceps femoris (vastus medialis, rectus femoris, vastus intermedius and vastus lateralis) during normal postures and locomotion (quadrupedal resting, walk/run, gallop and leaping) is presented for the brown lemur, *Lemur fulvus*. The vastus intermedius is the sole contributor to muscle recruitment during quadrupedal resting postures. It exhibits consistently high levels of electrical activity during all locomotory behaviour. The vastus medialis is recruited least among these muscles during walk/run and tends to be 'saved' for galloping and leaping. The rectus femoris and vastus lateralis are recruited at similarly high levels during all phasic activities. The rectus femoris appears to be used eccentrically, storing 'elastic strain energy' during all phasic activities. The vastus lateralis combines exceptionally high potential effective force with relatively high potential velocity and resistance to fatigue and probably develops the majority of force in all phasic activities. These results support previously documented structural and histochemical data that imply a functional division of labour among these muscle synergists.

INTRODUCTION

Previous studies of contractile properties of whole muscles have provided some insight into the physiological significance of fibre structure and fibre type composition (e.g. Burke *et al.* 1971; Goslow, Cameron & Stuart, 1977; Walmsley & Proske, 1981; Spector *et al.* 1980). Without direct observation of muscle activity in freely moving animals, however, realistic functional interpretations of such morphological features remain highly speculative. As a viable approach to this problem, electromyography (EMG) has evolved into a widely accepted methodology with which muscle recruitment patterns can be monitored accurately.

Key words: electromyography, fibre types, *Lemur fulvus*, muscles, quadriceps femoris.

Indeed, electromyographically identified recruitment patterns in muscle of known fibre type composition are consistent with general principles of intra- and inter-muscular organization (e.g. Betts, Smith, Edgerton & Collatos, 1976; Smith, Edgerton, Betts & Collatos, 1977; Botterman, Binder & Stuart, 1978; Walmsley, Hodgson & Burke, 1978; Smith, Betts, Edgerton & Zernicke, 1980; Gardiner, Gardiner & Edgerton, 1982; Anapol, 1984, 1985; Gorniak, 1986). For example, in extensor or antigravity groups, the most slowly contracting and most aerobic fibres are found in the highest percentages in muscles closest to the bone and in the deepest portions of mixed muscles. These muscles are thought to be recruited preferentially during posture and phasic behaviour of low intensity. Increasing intensity of behaviour would be accompanied by peripheral recruitment of fibres having successively lower oxidative capacities and faster contractile speeds (Walmsley *et al.* 1978; Armstrong, 1980; however, see Gillespie, Simpson & Edgerton, 1974).

In this study of primate locomotion, we present a quantitative analysis of electrical activity in the quadriceps femoris – vastus medialis (VM), rectus femoris (RF), vastus intermedius (VI) and vastus lateralis (VL) – of the brown lemur (*Lemur fulvus*) during normal postures and locomotion (quadrupedal resting, walk/run, galloping and leaping). In most mammals, the four heads of the quadriceps femoris are variably fused towards their distal insertion into the patellar tendon. In the brown lemur, however, the heads are completely separated (Jungers, Jouffroy & Stern, 1980). Furthermore, each muscle is characterized by a distinguishing constellation of structural and histochemical features that imply functional specialization during locomotion (Anapol & Jungers, 1986).

The present findings suggest that the characteristic levels of EMG in the muscles of this synergistic group during normal locomotion demonstrate functional 'division of labour'. This is correlated to the constellation of structural and histochemical features unique to each belly. Briefly, VM is a parallel-fibred muscle composed primarily of fast-twitch low-oxidative (F) fibres (Fig. 1). It is silent during posture, recruited the least of all muscles during walk/run, and appears to be 'saved' for galloping and leaping. RF is a bipinnate muscle also composed primarily of fast-twitch fibres, but a greater proportion of these are highly oxidative (FO). It may be contracting eccentrically during phasic behaviour, thereby storing 'elastic strain energy'. The predominantly slow-twitch high-oxidative (S) fibres of VI are unipinnately arranged with all fibres arising fleshily from the anterior surface of the femur. It is the only muscle of the group active during posture and continues to exhibit consistently high levels of EMG during phasic behaviour. Although VL is also unipinnate, its fasciculi extend between broad, tapering tendons on the superficial and deep surfaces of the belly; this allows highly circumscribed proximal and distal attachments of the whole muscle. Like RF, VL is predominated by fast-twitch fibres with a large proportion of FO. However, a statistically significant proportion of S fibres distinguishes VL from both VM and RF. VL probably develops the majority of force for all phasic activities.

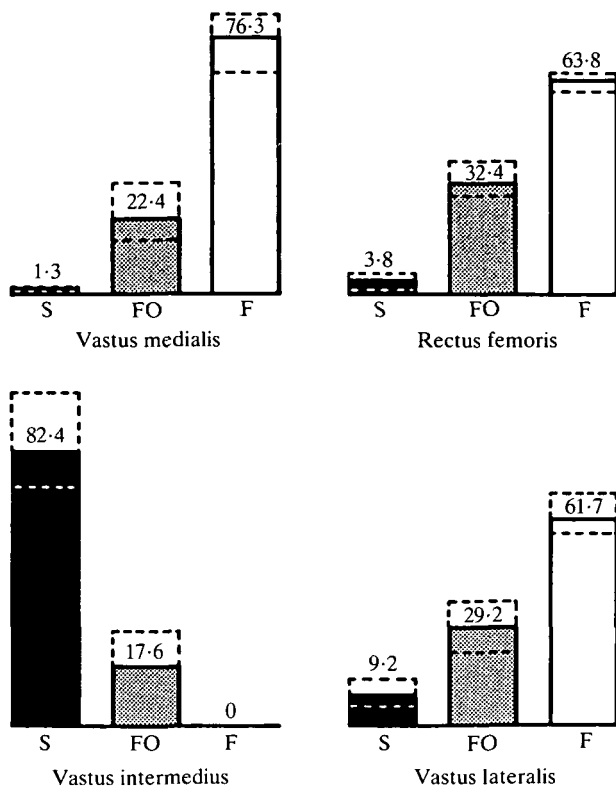


Fig. 1. Mean percentage of cross-sectional area for S (slow-twitch, high-oxidative), FO (fast-twitch, high-oxidative) and F (fast-twitch, low-oxidative) fibres in *Lemur fulvus*. Broken lines represent the range for three animals (adapted from Anapol & Jungers, 1986).

MATERIALS AND METHODS

In three healthy adult *Lemur fulvus*, electrical activity was recorded from the four heads of the quadriceps femoris while postural and locomotor activities were videotaped (following Stern, Wells, Vangor & Fleagle, 1977). Each subject was anaesthetized with halothane (3%)–oxygen/nitrous oxide (97%), and four ipsilateral muscles (VM, RF, VI, VL) were implanted with bipolar fine (50 μm) nylon wire electrodes with 1–2 mm bared ends (prepared according to the method of Basmajian & Stecko, 1962). Verification of electrode placement was achieved by passing a small stimulating current back to the muscle and observing both the contraction of the relevant muscle and the movement of the limb segment (Susman & Stern, 1979; Jungers *et al.* 1980).

Telemetered electromyography was employed to allow the postural and locomotory movements of the animal to occur free from the restrictions of wire attachments to more stationary recording devices. A four-channel frequency-modulated telemetry transmitter (Bio-Sentry Telemetry, Inc., Torrance, CA) was fastened to a waist belt and positioned against the subject's lower back. The telemetry system provided a gain of 1000 with a linear frequency response from 50 to 300 Hz. The gain fell by 3 dB

at 15 Hz and at 1150 Hz, which define the limits of the recording range in these experiments.

The electrical activity from each muscle was displayed on a Tektronix 5113 storage oscilloscope. While a television camera (Panasonic WV-341P) videotaped the animal's movements, a second video camera (Panasonic WV-260P) viewed the oscilloscope. A special effects generator (Panasonic WJ-545P) superimposed the oscilloscope display onto the video image, which was recorded on a Panasonic (NV-3130) videotape recorder (VTR) at 60 fields s^{-1} . Illumination of the subject was enhanced through the use of a Unitux (Lodi, NJ) Model 800 stroboscope fitted with a filter (Kodak Wrattan 89B) that only allowed passage of infrared frequencies. The camera could be modified to respond exclusively to these frequencies and the room could then remain lit with ordinary fluorescent bulbs while protecting the animal from blinding light (Stern *et al.* 1977).

Analysis of the videotape was accomplished by replaying the tape field-by-field and marking (on the monitor screen) the leading edge of the oscilloscope trace at four events during each step cycle: (1) *contact*, when the foot was initially placed upon the substrate to begin support (or stance) phase; (2) *mid-support*, during which a vertical line could be passed through the hip and metatarsophalangeal joints; (3) *release*, when the foot left the substrate to begin swing (or recovery) phase; (4) *mid-swing*, during which a vertical line could be passed through the hip and ankle joints. The intervals 1-2, 2-3, 3-4 and 4-1 closely correspond to phases designated for the cat step cycle (E_2 , E_3 , F, E_1) by Philippson (1905) and commonly applied by other investigators (e.g. Goslow, Reinking & Stuart, 1973; Wetzel & Stuart, 1977).

At the end of a complete EMG sweep (2 s duration), the image of the subject was momentarily blanked out and only the traces were displayed. A replicate of this was obtained with a Tektronix 4632 video hard copy unit interfaced to the VTR; the events from the screen were marked on the copy.

The behaviour that was analysed included quadrupedal resting (POS), walk/run (W/R), gallop (GAL) and standing high leaps (LP). Standing high leaps (approximately 2.3-3.3 m vertical from posture) were chosen for analysis in preference to other leaping activities (e.g. standing low leaps, running leaps) because (1) this was the most common leaping behaviour observed in two of the three subjects; (2) variability in total muscle use due both to the presence of a horizontal component and to momentum in the leap of a running animal could be ignored; and (3) the difficulty in training lemurs precludes the accumulation of homogeneous samples of 'experimenter-controlled' types of behaviour (e.g. leaping at specific, predetermined heights).

For POS, random intervals of equal duration were selected for quantification. For W/R and GAL, the interval between mid-swing (4) and release (3) of the subsequent step cycle was quantified (Fig. 2). This roughly corresponds to the entire extension portion (i.e. E_1 , E_2 and E_3) of Philippson (1905) and includes muscle activity in preparation for support, as well as support-phase activity *sensu stricto*. For LP, the interval from the onset of discernible vertical movement until the foot of the electrode-implanted limb left the substrate was quantified.

For each interval, the raw EMG trace (excluding isolated single spikes) was digitized (NT-501 Sonic Digitizer, Scientific Accessories Corporation Graf/Pen), and the x-y coordinates were transmitted to a DECLS-I 11/2 microcomputer (according to the method described by Stern *et al.* 1980). The amplitude was normalized as a percentage of the maximum burst recorded in the most strenuous activity during an experiment, and the temporal parameter was distributed equally among 20 equal columns. Each column was 'filled' (up to 20 rows high) to a level equal to the mean normalized amplitude of the EMG within the portion (i.e. 1/20) of the interval. The output for a single phase was composed of a 20×20 matrix in which a symbol appeared in all cells that corresponded to EMG activity; zeros were displayed in the remaining cells.

For each quadrupedal or leaping interval, the percentage of the area of an output matrix that corresponded to EMG activity was calculated. These 'percentages of maximum impulse' (IMP) were averaged (\pm standard deviation) for individual animals. 'Impulse' (*sensu stricto*) is defined as 'the area under a graph of force against time' (Alexander, 1974). However, close correlation between the change in levels of rectified, averaged EMG and the change in levels of force output measured directly at the tendon has been demonstrated, e.g. in medial gastrocnemius and soleus muscles during walking and running in the cat (Walmsley *et al.* 1978). Therefore, assuming that changes in electrical activity reasonably represent changes in muscular force output, we have chosen to refer to the area under the curve, metaphorically, as 'impulse'.

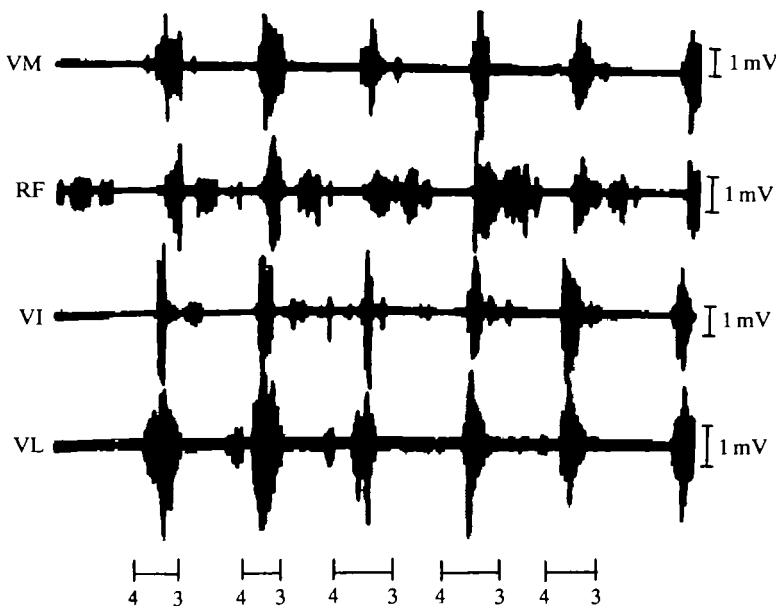


Fig. 2. Representative electromyograms (200 ms duration) of quadriceps femoris in *Lemur fulvus* while galloping quadrupedally on the ground. VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis; 4, mid-support; 3, release (see text) (adapted from Jungers, Jouffroy & Stern, 1980).

The maximum amplitude as a percentage of the height of a matrix was also calculated (AMP). For both IMP and AMP, the mean (\pm standard error) was calculated for a 'composite lemur' (CL), and significant differences between pairs of muscles during each class of behaviour were evaluated using Student's *t*-distribution (Sokal & Rohlf, 1981).

RESULTS

A qualitative assessment of electromyographic activity in the quadriceps femoris of the brown lemur is detailed elsewhere (see Jungers *et al.* 1980). A description of the recruitment patterns of muscles in the three lemurs (subjects A, male; B, female; C, male) during posture, branch quadrupedalism (walk/run), ground quadrupedalism (gallop) and leaping is briefly summarized below.

The vastus intermedius was the only muscle of the four which was consistently active during quadrupedal and bipedal POS. The vastus medialis, rectus femoris and vastus lateralis were generally silent during POS, although they sporadically elicited low-level activity. Regular, very low-level postural activity in RF occurred only in subject A. VM and VL were never active during POS in subject C.

During branch quadrupedalism, the lemurs walked and ran at speeds ranging from 325 to 495 ms per step cycle without changing gait; trotting was rarely observed. Electrical activity immediately preceded contact in VI and VL, but only occasionally in RF (only in subject A) and VM (only during the faster step cycles of subject C). This occurred when the hip approached maximum flexion and the knee approached maximum extension; in subject C, the knee did not become fully extended until after touchdown. At the beginning of support phase, the knee momentarily became slightly flexed (or 'yielded', i.e. E₂ of Philippson, 1905), then proceeded to extend until release. Throughout most of support, all four muscles were active as both the hip and knee were extending. From the end of support to mid-swing (3-4) (which approximates to F, or flexion phase, of Philippson, 1905), activity occurred only in RF and only at the slower speeds during hip flexion. In almost all cases the onset of activity in VI and VL slightly preceded that in VM and RF. Patterns of recruitment during ground quadrupedalism were generally similar to those of branch quadrupedalism. However, the more rapid ground quadrupedal cycles of subject B were characterized by an earlier onset of activity in VI and VL than during branch quadrupedalism.

Galloping was the predominant ground behaviour at speeds ranging from 171 to 204 ms per step cycle. The muscles first activated in galloping were VL and VI, followed by simultaneous bursts in RF and VM during mid-support. In subject C, a mid-swing burst was observed in VM during a step cycle slower than any observed in subjects A and B. This may have been an active contribution to knee extension that otherwise would result from momentum during the more rapid cycles. A recovery burst occurred in RF during swing-phase flexing of the hip.

Standing high leaps were characterized by marked increases in electrical activity in all muscles except VI. In one subject (A), a period of eccentric contraction (with

both the hip and knee flexing) preceded the upward propulsive phase. In subject B, considerable isometric tension preceded joint extension, presumably to enhance the muscular force output (Jungers *et al.* 1980, after Cavagna, Saibene & Margaria, 1965; Bergel, Brown, Butler & Zacks, 1972).

Subject C performed running high leaps in lieu of standing high leaps. The increase in EMG levels (over those of galloping) was not nearly as dramatic as the increase observed in the standing high leaps of subjects A and B. Besides the observation that running leaps were generally not as high as standing high leaps, the momentum of a running animal probably contributes to some of the work (*via* release of stored elastic energy) that otherwise requires active contraction when initiated from standing posture.

In Tables 1 and 2, mean IMP and AMP values for each muscle during behaviour of increasing intensity (POS < W/R < GAL < LP) are presented for three lemurs and CL (\pm standard error). These data are presented graphically in Figs 3 and 4 for CL (only). Leaping activity includes only standing high leaps for CL and subjects A and B. For subject C, leaping includes only running high leaps.

For CL, significant differences between means of all possible muscle pairs were determined for both IMP and AMP for each behaviour using Student's *t*-distribution (Table 3). For each pair, the results for both IMP and AMP generally coincided. However, in several cases (W/R: RF \times VL; GAL: RF \times VI, VI \times VL; LP: VM \times VL, VI \times VL), either the means for IMP *or* AMP, but not both, were significantly different. IMP is a function of both the duration and the amplitude of muscle activity during a 4–3 interval. Theoretically, of two muscles with similar means for IMP, one could be characterized by a longer duration and a significantly lower mean percentage maximum amplitude.

One of the most striking aspects of Figs 3 and 4 is the difference in recruitment between the slow-twitch, high-oxidative VI and the three fast, mixed muscles. During POS, VI reached the IMP value it maintained during all quadrupedal behaviour, while the remaining muscles elicited little or no muscle activity (Fig. 3). In VM, RF and VL, IMP was substantially greater during W/R and increased further during GAL, for which behaviour the values for all four muscles were similar. For LP, IMP in VM, RF and VL all surpassed that in VI.

During POS, AMP (Fig. 4) was dramatically higher in VI than in the other three muscles. However, the rate of increase of AMP in VI from POS to GAL was lower than the rates of increase in VM, RF or VL. At GAL, this disparity was greatly reduced. AMP values of VM, RF and VL all increased at generally equal increments from POS to LP.

Among the 'faster' three muscles (VM, RF, VL), three phenomena recurred. (1) During W/R, both IMP and AMP ($P < 0.1$, Table 3; Figs 3, 4) of VM were lower than either RF or VL. (2) During GAL, the means of VM, RF and VL were not significantly different for IMP or AMP. (3) During LP, the means of IMP ($P < 0.1$) and AMP (not statistically significant, $P > 0.1$) were lower in VL than in both VM and RF.

Table 1. *Percentage of maximum impulse: individual subjects and composite lemur (= mean)*

Muscle	Subject	N	Posture	N	Walk/run	N	Gallop	N	Standing high leap
VM	A	23	1.1	22	7.5	21	20.1	11	74.3
	B	22	0.6	19	15.4	17	28.5	7	79.2
	C	21	0.0	3	13.7	18	23.1	—	—
	Mean	66	—	44	—	56	—	18	—
	(Mean - s.e. - mean + s.e.)		0.6 (0.0-1.2)		12.2 (8.0-16.4)		23.9 (19.6-28.2)		76.8 (73.3-80.3)
RF	A	23	9.3	22	13.1	21	20.1	11	76.4
	B	22	1.6	19	16.5	17	26.5	7	78.8
	C	21	3.4	3	18.7	18	29.2	—	—
	Mean	66	—	44	—	56	—	18	—
	(Mean - s.e. - mean + s.e.)		4.8 (0.8-8.8)		16.1 (13.3-18.9)		25.3 (20.6-30.0)		77.6 (75.9-79.3)
VI	A	23	29.9	22	30.9	21	24.3	11	55.3
	B	22	20.7	19	26.4	17	27.7	7	50.8
	C	21	21.7	3	23.5	18	28.9	—	—
	Mean	66	—	44	—	56	—	18	—
	(Mean - s.e. - mean + s.e.)		24.1 (19.1-29.1)		26.9 (23.2-30.6)		27.0 (24.6-29.4)		53.1 (49.9-56.3)
VL	A	23	1.8	22	14.1	21	20.6	11	67.2
	B	22	1.7	19	20.5	17	28.3	7	68.3
	C	21	0.0	3	19.2	18	28.1	—	—
	Mean	66	—	44	—	56	—	18	—
	(Mean - s.e. - mean + s.e.)		1.2 (0.2-2.2)		17.9 (14.5-21.3)		25.7 (21.3-30.1)		67.8 (67.0-68.6)

VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis.

Table 2. Percentage of maximum burst amplitude: individual subjects and composite lemur (= mean)

Muscle	Subject	N	Posture	N	Walk/run	N	Gallop	N	Standing high leap
VM	A	23	3.5	22	22.0	21	69.5	11	94.3
	B	22	2.3	19	36.3	17	86.2	7	100.0
	C	21	0.0	3	26.7	18	58.9	—	—
	Mean (Mean - S.E. - mean + S.E.)	66	1.9 (0.0-3.7)	44	28.3 (21.0-35.6)	56	71.5 (57.7-85.3)	18	97.1 (92.9-100.0)
RF	A	23	12.4	22	33.4	21	60.7	11	96.8
	B	22	4.1	19	37.6	17	74.1	7	99.3
	C	21	6.0	3	50.0	18	65.6	—	—
	Mean (Mean - S.E. - mean + S.E.)	66	7.5 (3.2-11.8)	44	40.3 (31.7-48.9)	56	66.8 (60.0-73.6)	18	98.1 (96.3-99.9)
VI	A	23	38.9	22	72.3	21	82.9	11	90.5
	B	22	33.6	19	58.2	17	91.2	7	85.0
	C	21	31.2	3	58.3	18	80.0	—	—
	Mean (Mean - S.E. - mean + S.E.)	66	34.6 (30.7-38.5)	44	62.9 (54.8-71.0)	56	84.7 (78.9-90.5)	18	87.8 (83.9-91.7)
VL	A	23	4.1	22	32.5	21	59.3	11	92.3
	B	22	2.7	19	39.5	17	77.4	7	97.1
	C	21	0.0	3	41.7	18	64.4	—	—
	Mean (Mean - S.E. - mean + S.E.)	66	2.3 (0.2-4.4)	44	37.9 (33.1-42.7)	56	67.0 (57.7-76.3)	18	94.7 (91.3-98.1)

VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis.

As a consequence of crossing both hip and knee joints, RF was active at least part of the way into late swing phase (4-1) during W/R (but at a lower amplitude than that attained during support). This effectively inflated its IMP value but not its AMP value. During GAL, this swing-phase activity ended before mid-swing and was excluded from the measured 4-3 interval.

As the intensity of locomotory behaviour increased (i.e. POS → GAL), the co-occurrence of a relatively high rate of increase for AMP with a lower rate for IMP indicates a shift from reliance upon low-level muscle activity for extended durations to that of short, intense bursts during otherwise 'silent' step cycles. The lower (relative to IMP) rate of increase of AMP from GAL to LP resulted from the longer duration, with amplitude either remaining constant (as in VI) or increasing at a slower rate than the duration (as in VM, RF, VL). In other words, the amplitudes of VM, RF and VL increased from POS to GAL, while their durations were decreasing; from GAL to LP, both their amplitudes and durations increased. By contrast, while the duration of VI increased considerably from GAL to LP, the amplitude remained virtually the same. This suggests a relatively narrow range of recruitment in that VI was almost fully recruited for GAL with little reserve left for standing high leaps.

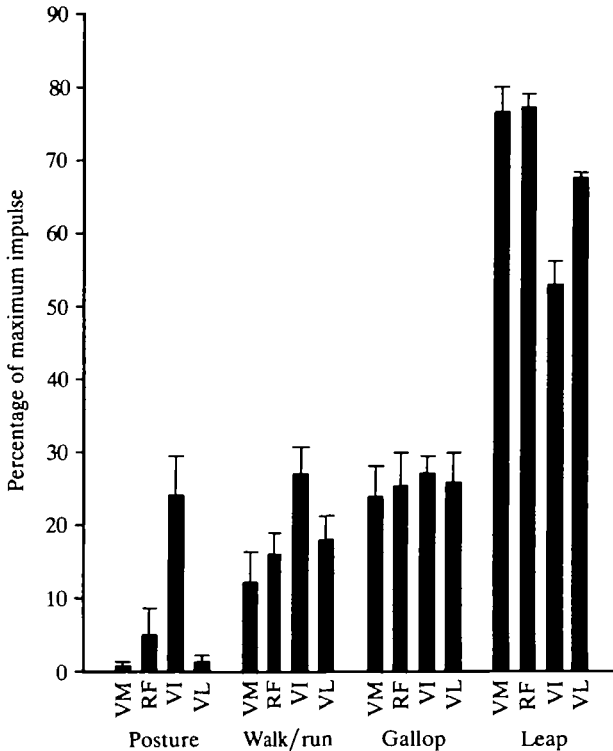


Fig. 3. Mean percentage maximum impulse for composite lemur (see Table 2 for numerical values for composite lemur and individual subjects). VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis.

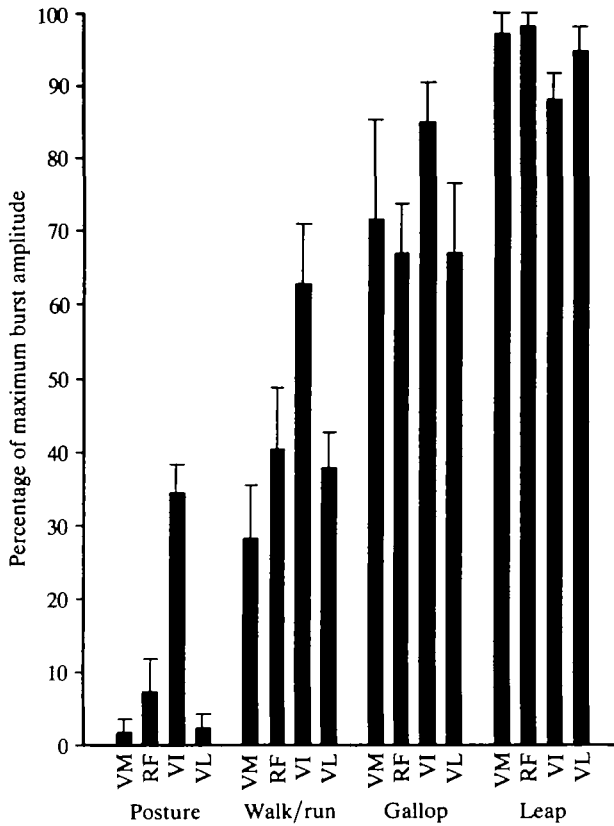


Fig. 4. Mean percentage maximum burst amplitude for composite lemur (see Table 3 for numerical values for composite lemur and individual subjects). VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis.

Table 3. Results of tests for significance of differences ($P < 0.1$) between means for all possible pairs of muscles (derived from Student's *t*-distribution)

Muscle pair	Posture (d.f. = 130)		Walk/run (d.f. = 86)		Gallop (d.f. = 110)		Leap (d.f. = 34)	
	IMP	AMP	IMP	AMP	IMP	AMP	IMP	AMP
VM×RF	0.1	0.1	0.1	0.1	NS	NS	NS	NS
VM×VI	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
VM×VL	NS	NS	0.1	0.1	NS	NS	0.1	NS
RF×VI	0.1	0.1	0.1	0.1	NS	0.1	0.1	0.1
RF×VL	0.1	0.1	0.1	NS	NS	NS	0.1	0.1
VI×VL	0.1	0.1	0.1	0.1	NS	0.1	0.1	NS

d.f., degrees of freedom; NS, no significant difference at $P < 0.1$.

IMP, percentage of maximum impulse; AMP, percentage of maximum amplitude; VM, vastus medialis; RF, rectus femoris; VI, vastus intermedius; VL, vastus lateralis.

DISCUSSION

The electromyographic signal is not a direct measurement of a muscle's force output, but rather an 'electrical manifestation of the neuromuscular activities associated with a contracting muscle' (DeLuca, 1979, p. 53). Nevertheless, close correlation between EMG and force directly measured at the tendon has been demonstrated in, for example, cat medial gastrocnemius and soleus muscles (Walmsley *et al.* 1978). Although *duration* is thought to be a more reliable parameter of the EMG trace than *amplitude* (Rasmussen, Chan & Goslow, 1978), reason would dictate that higher amplitude reflects increased force either by more rapid neuronal firing frequency or by the recruitment of additional motor units (however, see Gans & DeVree, 1986). Because of the extraordinary number of variables that must be considered in recording the EMG signal, the analysis must focus upon *relative changes* in level of activity normalized to some standard, rather than absolute voltages.

Current technology is unable to discriminate accurately among electrical signals from different classes of motor units within mixed whole muscles. However, differences in EMG recruitment patterns between whole muscles and regions within a muscle have been correlated to differences in relative percentages of the three general classes of fibre type which compose those muscles or regions (Smith *et al.* 1977, 1980; Botterman *et al.* 1978; Walmsley *et al.* 1978; Gardiner *et al.* 1982; Anapol, 1985; Gorniak, 1986). Interpretation of the EMG results may be further complicated by the presence of intramuscular compartmentalization (Herring, Grimm & Grimm, 1979; English & Letbetter, 1982; Herring & Wineski, 1986). The muscles considered here were not compartmentalized and each whole belly could be characterized by a mean value. Interanimal variation was not of a magnitude that would significantly alter the interpretation of the results.

Vastus medialis

Of the four muscles, the structural and histochemical characteristics of the vastus medialis indicate that it would (1) develop the least effective tetanic tension, (2) contract with the highest velocity, (3) conserve the least amount of energy and (4) attain maximum tension of the whole muscle in the least amount of time (Anapol & Jungers, 1986). VM was never recruited during posture. During W/R, it was recruited at a lower percentage of maximum burst than the other three heads. During galloping, VM was recruited at a level equal to or higher than the other 'fast' muscles (RF and VL) and surpassed the activity level attained by VI during standing high leaps.

Morphologically, VM is specialized for rapid recruitment and appears to be 'saved' to augment the most dynamic locomotory activities with a later surge of force. In this regard, it need not be adapted for 'energy savings', such as is required by behaviour that is more of the endurance type (e.g. POS and W/R). The low ratio of tendon length to fasciculus length minimizes its ability to store elastic strain energy (Alexander, 1974; Biewener, Alexander & Heglund, 1981). By contrast, the potential

velocity of VM is maximized by the presence of contractile material almost the entire length of the muscle. In addition, VM consists predominantly of fast-twitch, high-oxidative fibres. Current theory of motor unit recruitment suggests that primarily S- and FO-type motor units are recruited for posture and during behaviour as vigorous as fast running. F-type fibres are more or less reserved for the most intense forms of locomotion, such as galloping and leaping (Gillespie *et al.* 1974; Walmsley *et al.* 1978; Armstrong, 1980).

Rectus femoris

Structural and histochemical features of the rectus femoris predict a potential for (1) development of moderate effective tetanic tension, (2) contraction with the lowest velocity (shortest whole muscle excursion), (3) the greatest energy conservation and (4) rapid attainment of nearly maximal recruitment levels which may be sustained for an extended period. RF displayed intermediate levels of muscle activity during all quadrupedal behaviour, and (with VM) the highest activity of all muscles during standing high leaps.

Although RF is the only muscle of the quadriceps femoris long enough to cross two joints, its calculated maximum excursion is the lowest of the four (Anapol & Jungers, 1986). RF may be functioning as a 'stiff spring' (Taylor, 1978) in order to store elastic strain energy. During early support phase, simultaneous hip extension and knee flexion stretched the loaded RF. As a muscle lengthens while force is exerted upon it, energy can be stored both in the tendons (Alexander, 1974; Biewener *et al.* 1981) and to a lesser degree in the elastic extension of the cross-bridges (Cavagna, Citterio & Jacini, 1980). The bipinnate arrangement of the fasciculi provides a relatively high number (per gram of mass) of tendon-fasciculus-tendon elements in parallel. During late support, extension of the knee allowed RF to shorten, thereby releasing the stored energy for forward propulsion. This propensity for energy conservation would be advantageous for a muscle, such as RF, that is active both in support phase for knee extension and swing phase for hip flexion during a single step cycle. In addition, the high proportion of FO fibres could allow repetitive eccentric contractions to occur rapidly for extended periods.

Vastus intermedius

The morphological attributes of the vastus intermedius indicate that it would (1) develop substantial effective tetanic tension, (2) contract with low velocity (short excursion), (3) conserve a relatively high amount of energy and (4) be the earliest muscle to attain high levels of recruitment, with an ability to sustain tension for an extended period. VI accomplished its highest percentage of EMG activity during POS. This level was maintained during W/R and GAL, but was surpassed by VM, RF and VL during standing high leaps.

In VI, the level of EMG activity is independent of the behavioural mode as well as the speed of the animal during the behaviour (Anapol, 1984). It is the only muscle of the quadriceps femoris that is recruited during posture. These results are consistent

with previously reported observations of other 'postural' muscles, e.g. the soleus in cat (Walmsley *et al.* 1978) and guinea-pig (Gardiner *et al.* 1982).

VI maintains a consistently high level of EMG throughout all behaviour, further demonstrating positive correlation between the proportion of slow fibres and the time for which a muscle is active (as in humans, Monster, Chan & O'Connor, 1978). During LP, EMG activity surpassed levels attained for posture and quadrupedal behaviour. This extended range of recruitment may be the result of a substantial proportion of FO fibres (Anapol, 1984; Anapol & Jungers, 1986).

Within the quadriceps, VI is the muscle most clearly suitable for postural behaviour. It is composed entirely of highly oxidative muscle fibres, most of which are characterized by acid-stable myosin adenosine triphosphatase reactivity. This histochemical fibre type has been correlated to slow speeds of contraction and low susceptibility to fatigue (Burke *et al.* 1971; McDonagh, Binder, Reinking & Stuart, 1980). The morphology of VI predicts that substantial tension is developed slowly and can be sustained extensively at small changes in length.

Subject B accomplished a standing high leap after only momentarily contacting the substrate when landing from the preceding leap. She had failed to gain an adequate foothold and recovered by immediately launching into the second leap. During the second leap, VI elicited relatively lower and more erratic EMG activity than the typically high levels reached during 'normal' leaps. By contrast, the quality of the signals from VM, RF and VL were relatively unaffected, being only slightly reduced in overall amplitude. Thus, stabilization of joints for support in behaviour of a predominantly phasic type may be effected by preferential recruitment of deep, slow postural muscles (Smith *et al.* 1977). This example represents a deviation from the 'size principle' (Henneman & Olson, 1965), which requires slow motor units (small surface area of alpha motoneurons) to be recruited before faster units (large surface area). By contrast, the observed EMG pattern of the aberrant leap suggests selective inhibition of slow motor units with deference to faster units for sudden, rapid or especially dynamic movements (Smith *et al.* 1977, 1980; Gillespie *et al.* 1974; Armstrong *et al.* 1977; Sullivan & Armstrong, 1978).

Vastus lateralis

Among the four muscles, vastus lateralis could (1) develop the highest effective tetanic tension, (2) contract with the second highest velocity, (3) conserve a relatively high amount of energy and (4) recruit a substantial proportion of its cross-sectional area in behaviour of widely varying intensities (Anapol & Jungers, 1986). VL exhibited a substantial level of EMG during all quadrupedal locomotory behaviour.

VL is the 'work horse' of this muscle group. Its enormous mass is distributed over the entire spectrum of fibre types, providing a dimension of flexibility to its effective range of recruitment. While constituting nearly 60% of the combined mass of the group, VL embodies force, velocity, economy and endurance.

By contrast to VM, VL has approximately 8% more S-type fibres and is recruited at higher EMG levels during W/R. VM, however, has 14.6% more F-type fibres than VL. This may account for the 'late acceleration' phenomenon of VM during the

more intense types of behaviour (i.e. GAL, LP) when it approaches or exceeds the EMG levels of VL.

Despite remarkable disparity in both potential effective tetanic force and potential velocity, RF and VL exhibit relatively similar levels of EMG during all quadrupedal behaviour. This may be explained by the similarity in their elastic and fibre type characteristics. Of the quadriceps, they have the highest ratios of tendon length to muscle fasciculus length and the highest proportion of FO fibres (Anapol & Jungers, 1986). These qualities are related to energy conservation and endurance and their occurrences in muscles which bear substantial portions of the workload would appear to be essential. VL attains a significantly higher IMP during W/R than does RF, probably a result of a population of S fibres (in VL), but lower IMP and AMP levels during standing high leaps.

By contrast to VM and RF, VL was not nearly expended during standing high leaps (Fig. 3) and its structure further supports gross anatomical evidence of its suitability for leaping (Stern, 1971). First, pinnation allows a dramatic increase in the number of fasciculi (i.e. the number of cross-bridges in parallel) and, therefore, in the total force that can be applied through the tendon of insertion.

Second, although the lengths of the pinnately arranged fasciculi are limited by the geometry of the thigh, they are substantially longer than the fasciculi of the other pinnate muscles (RF and VI). In addition, the whole muscle excursion of a pinnate muscle is proportionately greater than the shortening of its constitutive fasciculi, and greater than that of a parallel-fibred muscle with the same fasciculus length (Gans & Bock, 1965; Gans, 1982; Muhl, 1982). Increasingly longer fasciculi (whether pinnate or parallel) are able to generate equivalent excursions with less shortening per sarcomere. Consequently, the longer fasciculi can maximize the length-tension relationship by remaining within a range of greater thin-thick filament overlap (Muhl, 1982). Thus, the long pinnate fasciculi of VL can combine great tension with high velocity.

Third, the superficial and deep surfaces of VL are covered by the tendons of origin and insertion. This results in proximal and distal 'suspension' of the fasciculi between elastic elements in series (Anapol & Jungers, 1986). The contiguous tendons can be held rather tautly by contraction of the muscle fibres. This would allow substantial storage of elastic strain energy when the knee is flexed (such as in the preparation for a leap). Electromyographic activity during eccentric contraction prior to the onset of a leap has been described previously (Jungers *et al.* 1980). Overall; the structure of VL in *L. fulvus* probably allows the greatest packing of fasciculi (for force), with the least sacrifice of length (for velocity), and at a relative reduction in requisite energy cost.

Thus, the four heads of the quadriceps femoris in *L. fulvus* exhibit patterns of electromyographic activity during normal locomotion that suggest a functional 'division of labour' among these muscle synergists. These results support earlier predictions of muscle function and specialization based on structural and histochemical findings (Anapol & Jungers, 1986).

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