The distal hindlimb musculature of the cat: multiaxis moment arms at the ankle joint

R.P. Young, S.H. Scott, G.E. Loeb

MRC Group in Sensory-Motor Physiology and Bio-Medical Engineering Unit, Queen's University, Kingston, Ontario, Canada K7L 3N6

Abstract. The cat hindlimb muscles have been classified, traditionally, as flexors and extensors, based on their actions in the parasagittal plane and their patterns of recruitment during locomotion and reflex responses. This study provides a detailed examination of the relative magnitudes of the various moment arms of the cat ankle muscles and the interdependent effects of position in the various axes of motion. We used a method based on observing small sliding movements of tendon in response to small angular displacements of the joint. Surprisingly, we found that the ankle joint of the cat permits substantial motion in three axes (eversion/inversion and abduction/adduction as well as extension/flexion) and many muscles crossing the ankle joint have their largest moment arms about axes other than extension/flexion. These moment arms often depended on the joint position in the axis of the moment arm and, to a lesser degree, on the extension/flexion angle as well. For some muscles (notably peroneus longus) there was sufficient variability that the predominant action in neutral posture (axis with the largest moment arm) could change from animal to animal, which may be related to heterogeneities of locomotor and reflex recruitment reported in the companion paper.

Key words: Muscles – Ankle – Moment arm – Cat

Introduction

When the nervous system commands a movement, either through reflex or voluntary control, the results depend on the intrinsic mechanical properties of the musculoskeletal system. Therefore, a full understanding of the neural mechanisms underlying the control of any motor behavior depends upon a thorough understanding of musculoskeletal structure and function.

The contractile force generated by a muscle produces skeletal motion by producing torques about the joints

Correspondence to: G.E. Loeb, Abramsky Hall, Queen's University, Kingston, Ontario, Canada K7L 3N6

that are spanned by the muscle. The torque produced by a muscle is the product of its tension (active and passive) and its moment arm at the joint in question (see Fig. 1). The moment arm is given by the distance from the joint center to the line of action of the muscle. This vector can be decomposed into components that correspond to the anatomical degrees of freedom. It is also the case that the amount of tension that can be generated by a muscle depends on the length and velocity of its sarcomeres, which in turn depends on the position and motion of the joints that it crosses, acting through the moment arms at those joints. Thus the nature and amount of work that a given muscle can do on the skeleton depends at least as much on the exact course of its tendons around each joint as it does on the cross-sectional area of the muscle.

The feline ankle is a typical joint, in that it has numerous muscles which act upon multiple degrees of freedom. The muscles crossing this joint traditionally have been considered to act in the main axis of motion during locomotion, plantar-flexion/dorsi-flexion (here designated physiologically as extension or flexion, respectively; Abraham and Loeb 1985; Crouch 1969). Secondary consideration is usually given to eversion/inversion (rotation along the long axis of the foot). In a preliminary report (Young et al. 1992), we have described a surprisingly large range of motion and large muscle moment arms in abduction/adduction (rotation of the foot with respect to the long axis of the shank). By comparison, abduction/adduction of the human foot does not occur in the ankle joint itself, but in the talonavicular joint of the foot (where it is coupled to eversion/inversion) and in rotation of the tibia (about its long axis) at the knee (Levens et al. 1948). In this report, we describe in detail the relative moment arms in each of these three axes for all of the muscles that cross the ankle joint. In particular, we have examined the changes in moment arms that occur as the joint is moved over the range of motion in the axis of the moment arm and simultaneously, in an orthogonal axis. We have also described surprisingly large variability between specimens in the relative actions of some of these muscles, which may relate to variability in their physio-
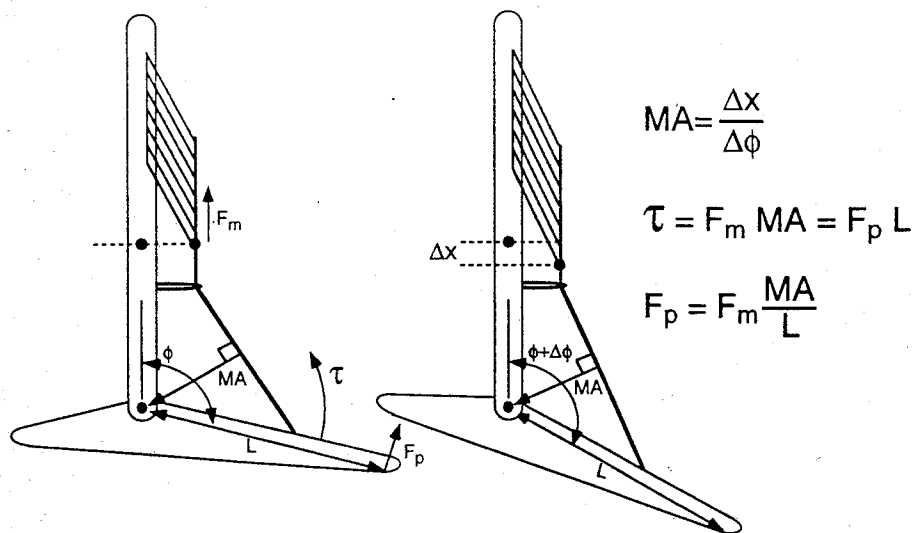
$$MA = \frac{\Delta x}{\Delta \phi}$$

$$\tau = F_m \, MA = F_p \, L$$

$$F_p = F_m \frac{MA}{L}$$

Fig. 1. The relationship between moment arm (MA), change in joint angle ($\Delta\phi$), and change in muscle length (Δx). The position of a point on the muscle relative to the tibia is recorded at a joint angle ϕ and at an angle $\phi + \Delta\phi$. The moment arm of the muscle equals the change in muscle length divided by the change in joint angle (in radians). The amount of torque (τ) generated by a muscle spanning the ankle joint is the product of the muscle's force (F_m) and its moment arm about the ankle joint. The force transmitted to the end of the foot (F_p) equals the muscle force (F_m) multiplied by its moment arm about the ankle joint and divided by the length of the foot (L)
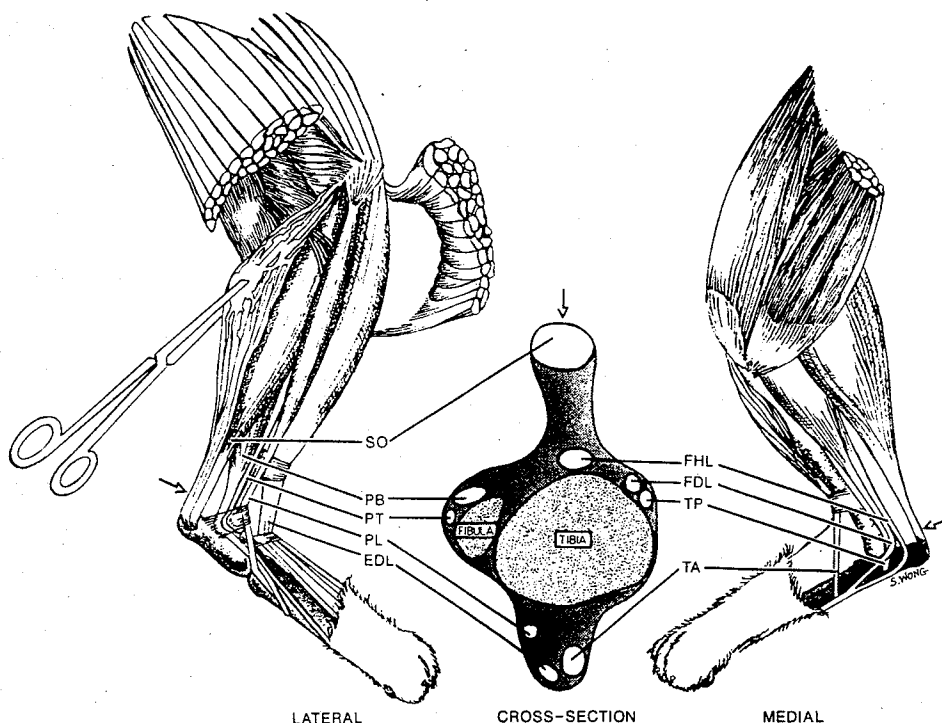

LATERAL   CROSS-SECTION   MEDIAL

Fig. 2. Anatomy of the feline ankle musculature. Left, lateral view of the leg and ankle; middle, cross-section of the ankle at the level of the malleoli; right, medial view of the leg and ankle. Muscle abbreviations: PL, peroneus longus, PB, peroneus brevis, PT, peroneus tertius, TP, tibialis posterior, FDL, flexor digitorum longus, FHL, flexor hallucis longus, TA, tibialis anterior, EDL, extensor digitorum longus, and SO, soleus

logical recruitment described in the companion paper (Loeb 1993).

Figure 2 shows gross anatomical views of the course of the muscles studied and their tendons about the ankle. A cross section was taken through the medial and lateral malleoli, the anatomical landmarks that denote the approximate center of rotation in flexion/extension. It shows that many of these muscles lie very close to this presumed center of rotation, so that any attempt to estimate moment arm from direct anatomical measurements would be very sensitive to small errors in locating the exact center of rotation, which may not even be fixed over the anatomical range of motion. Moment arms in the other axes depend on the often oblique course of these tendons through the retinacula and over the boney pulleys of the distal tibia, fibula, and tarsal bones, which cannot be appreciated in two-dimensional views. There-

fore, moment arms were computed from the tendon displacements measured during small increments of motion applied to each anatomical axis (An et al. 1983, 1984; Spoor and Van Leeuwen 1992; Spoor et al. 1990; Young et al. 1992). This technique makes no assumptions regarding the actual location, unicentricity, or even concentricity of the centers of rotation for each degree of freedom.

Materials and methods

The moment-arm data reported here are from 19 cat preparations (adult animals of either sex). An additional six animals had been used in preliminary studies to refine the experimental technique and one cadaver of similar mass (described below) was used to survey the musculotendinous architecture of these muscles. The animals were deeply anesthetized with intraperitoneal pentobarbital sodium

Table 1. Muscles and their path length changes

Muscle	Abbreviation	Mass (g)	Fasc[a] (mm)	ΔEx/Fl (mm)	ΔEv/Iv (mm)	ΔAb/Ad (mm)	ΔLPsum (mm)	FS
Peroneus longus	PL	1.81	12.8	4.8	1.6	3.9	10.3	0.80
Peroneus brevis	PB	1.05	8.8	0.3	1.8	4.1	6.2	0.70
Peroneus tertius	PT	0.47	12.0	0.7	2.0	3.0	5.7	0.48
Tibialis posterior	TP	1.16	5.2	0.6	0.3	4.3	5.2	1.00
Flexor digitorum longus	FDL	1.56	17.0	3.0	1.4	3.6	8.0	0.47
Flexor hallucis longus	FHL	5.10	15.6	8.3	0.6	1.4	10.3	0.66
Tibialis anterior	TA	7.41	49.1	15.8	2.6	1.3	19.7	0.40
Extensor digitorum longus	EDL	3.65	25.3	19.0	1.7	2.0	22.7	0.91
Soleus	SO	2.93[a]	33.5	22.0[b]			22.0[b]	0.66
Medial gastrocnemius	MG	10.58[a]	19.7	22.0[b]			22.0[b]	1.12
Lateral gastrocnemius	LG	11.65[a]	18.4	22.0[b]			22.0[b]	1.19

FS, fascicle stroke (ΔLPsum/Fasc) where ΔLPsum is the sum of length changes possible in each of the three anatomical axes: Ex/Fl, extension/flexion; Ev/Iv, eversion/inversion; Ab/Ad, abduction/adduction; Fasc, fascicle length;
[a] Obtained from 2.8-kg cat; sarcomere length normalized to 2.3 μm

[b] Moment arm was measured only for soleus and only about the Ex/Fl axis; we assumed that there is no significant moment arm about the other axes and that the other muscles contributing to the common Achilles tendon have a similar range of motion

and, as required, further doses of pentobarbital sodium were administered intravenously. At completion of the experiment, the animals were killed with an overdose of anesthetic.

In each animal, the moment arms of one to four muscles were measured through the full range of joint motion. Moment arms were measured about all three anatomical degrees of freedom for all of the ankle muscles whose names and abbreviations are listed in Table 1.

Moment arms from incremental motion

We built an apparatus that allowed us to make precise increments in joint angle about each of the three axes, while preventing motion about the other two axes (see Young et al. 1992). The connection between the foot clamp and the goniometers allows a small amount of sliding motion to prevent subluxating the joint even if the axes of rotation of the apparatus are not aligned precisely with the anatomical centers of rotation of the joint. The tendon-displacement technique involves making precise increments in joint position and measuring the resulting tendon motion with respect to a stationary bone (moment arm in millimeters = tendon motion in millimeters/joint displacement in radians; see Fig. 1). We used sonomicrometry (Triton Technology; as used in limb muscles by Griffiths 1987, and Hoffer et al. 1989) to measure precisely the tendon motion during these joint displacements. Sonomicrometry computes absolute distances from the transit time through saline of an ultrasound pulse between a transmitter-receiver pair of piezoelectric crystals. We were able to avoid uncertainties in the transmission velocity through soft tissue by directing all of the ultrasound paths through a saline pool (see below).

The skin of the leg and ankle was incised along either its medial or lateral aspect. The skin was then blunt-dissected free from the leg along all aspects in order to form a saline pool in which the muscle and crystals were maintained at body temperature by a thermostatically controlled heater. The muscle of interest was dissected free from surrounding connective tissue, but with origin and insertion and its nerve and blood supplies left intact. Also, soft tissue attachments which define the path of the muscle and tendon, along with other muscles sharing these constraints, were left intact, as their removal would have altered moment arm measurements.

The leg was suspended from two bone screws threaded into the tibia, perpendicular to the sagittal plane, plus one through the fe-

mur fixing the knee at an angle of 90–100°. The transmitting piezoelectric crystal was positioned along the line of pull of the muscle and attached rigidly to one of the tibial bone screws, thereby fixing it with respect to the shank. The receiving piezoelectric crystal was affixed to a small piece of polyester- (Dacron)-reinforced pliable plastic (Silastic) sheet that was sutured to the external tendon (i.e., distal to any aponeurosis) of the muscle of interest. Therefore, changes in the distance between the transmitter-receiver pair reflected sliding motion of the tendon with respect to the tibia. The tendons were normally slack for many joint positions, so we applied 200 g of tension to the tendon, along its line of action and proximal to the crystals, to remove any slack. This ensured that any joint motion was relayed to the tendon.

Extension/flexion moment arms were measured at 10° increments about the flexion/extension axis, with neutral taken to be 110°, the functional standing angle (Goslow et al. 1973). Abduction/adduction and eversion/inversion moment arms were each measured at 10° increments about the abduction/adduction and inversion/eversion axes, respectively, for extension/flexion angles (every 20°) within the joint's range of motion (typically, 70°, 90°, 110°, 130°, 150°). Larger increments (20°) about the abduction/adduction and inversion/eversion axes produced similar moment arms, while smaller increments resulted in displacements that were too small to be quantified accurately by the sonomicrometer (nominal resolution 0.04 mm).

Validation of moment arm measurements

The moment arm measurements were validated over the range of extension/flexion motion by comparing the results of the method described above with two other techniques. For both validation techniques, the foot was clamped to a strain-gauge apparatus, which measured a composite ankle torque (extension/flexion torque + eversion/inversion torque). The leg was suspended from the bone screws with the heated saline bath in place.

For the first validation technique, we substituted active muscle contraction for the passive tension applied to remove the slack in the tendons. The sciatic nerve was ligated proximally and a large cuff electrode was applied distal to the ligature. Joint displacements were applied as before, but at each extension/flexion joint position, the sciatic nerve was stimulated with a single pulse at 4 times threshold to remove slack of all ankle muscles. The nerve to the
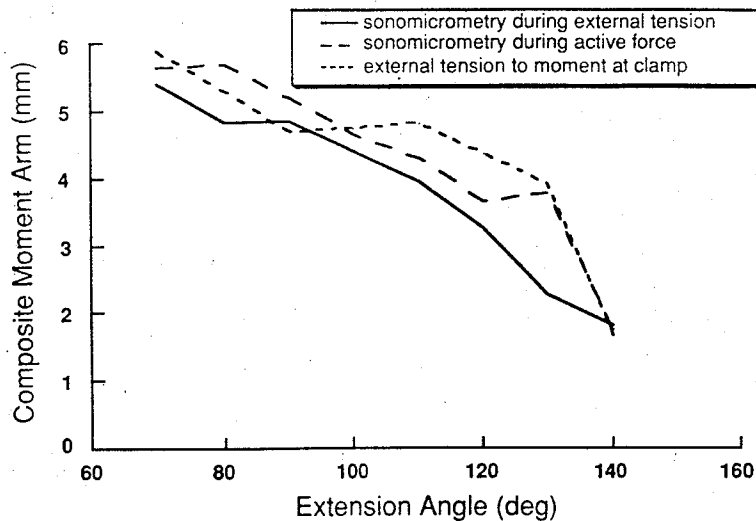
Fig. 3. The moment arm measures collected using the tendon and joint displacement method (An et al. 1983, 1984; Spoor et al. 1990; Spoor and Van Leeuwen 1992; Young et al. 1992), referred to here as sonomicrometry during external tension, along with data collected using the two validation techniques (see text for full description) are presented for peroneus longus 19 (PL19). For the former of these, sonomicrometry was used to measure tendon motion during active stimulation of the muscle of interest's nerve branch. The other validation technique involved examining the mechanical advantage of the muscle of interest by applying external tension to its tendon and recording the moment produced at the ankle, using a strain gauge which recorded a composite flexion-eversion moment. Composite moment arm, therefore, refers to the sum of the flexion and eversion moment arms

muscle of interest was then stimulated tetanically at 4 times its threshold to elicit a maximal contraction while we recorded sonomicrometrically the distance between the crystals on the tibia and the tendon. We simultaneously measured the length of the tendon itself via another pair of crystals, in order to correct for the different amounts of stretch that could result from different tensions produced by the muscle at different lengths.

In the second validation technique we determined the mechanical advantage of the lever and fulcrum formed by the foot and ankle joint. Calibrated tensions of 200 g and 400 g were applied proximally to the tendon and the resulting force on the strain gauge was recorded. Given the distance from the joint center to the strain gauge, the moment arm of the tendon about the joint center was computed from the ratio of the two forces (see Fig. 1).

Moment arms recorded using our primary method were summed (i.e., extension/flexion moment arm + eversion/inversion moment arm) for comparison with the composite moment arms produced using the validation techniques. As Fig. 3 demonstrates, all three techniques produced similar moment arm estimates. The small differences between them suggest an uncertainty of less than 1 mm, somewhat larger than the noise level for repeat measurements with a single technique (see below). However, the two validation techniques involve more indirect measurements of moment arm than the primary method of this study and may be more prone to error. Most muscles had primary moment arms of 5–15 mm. In general, we found that the reproducibility of repeat measurement sequences with a given technique in a given preparation was better than 10% or 0.3 mm (whichever was larger). In the following discussion, we have assumed that moment arm values of less than 1 mm are poorly characterized and probably mechanically insignificant.

Muscle morphometry

The technique used to measure moment arms often damaged the muscles too much to obtain accurate data on musculotendinous architecture beyond simple mass (provided in Table 1), so an additional cat of comparable mass was obtained from an unrelated study. Prior to being killed by pentobarbital overdose, the cat's knee was stabilized at an angle of approximately 100° and the ankle was stabilized with all axes at neutral joint angles (0° abduction and eversion, 110° extension). After rigor mortis was established, all ankle muscles were carefully removed from origin to insertion. Muscles mass was measured (excluding external tendon), along with fascicle lengths. These values plus others derived from the moment arm study are summarized in Table 1, and their functional implications are considered in the Discussion. Fascicle length was obtained by averaging a number of measurements from various regions of the

muscle, as many of the ankle muscles contain multiple neuromuscular and anatomical compartments (as revealed by stimulating individual nerve branches to a muscle and/or staining for motor end plates). Sarcomere length was also measured, allowing all fascicle lengths to be normalized to a constant sarcomere length of 2.3 μm. A few fascicles from various compartments of each muscle were mounted on slides; the number of sarcomeres required to span an 88-μm-wide microscope field was counted in each of five regions of each fascicle to obtain a mean value.

Results

Mean moment arm-joint angle profiles

The mean moment arms of each muscle about each anatomical axis are plotted, as a function of joint angle, in Fig. 4, allowing individual muscles to be classified by relative action. Muscles that typically have been considered to be the prime movers of the ankle during locomotion indeed have large moment arms in flexion (tibialis anterior, TA) or extension (triceps surae) – we have shown, previously, that the moment arm for soleus (SO) ranges from 7–15 mm throughout the joint's range of motion (Young et al. 1992). The moment arm profiles for these muscles have broad maxima at mid-range that decrease, but remain large, for extreme joint positions of both flexion and extension. Some other muscles that include multiarticular action on the digits also had substantial moment arms in ankle flexion (extensor digitorum longus, EDL) and extension (flexor hallucis longus, FHL). Peroneus longus and flexor digitorum longus (PL and FDL) also had significant moment arms in flexion and extension, respectively, but only at joint angles at which the muscles were shortened (note positive slope of both curves). The remaining muscles examined (peroneus brevis, peroneus tertius, tibialis posterior: PB, PT, TP) had negligible moment arms about the flexion/extension axis.

In abduction/adduction, all muscles had moment arms that increased as the muscle was stretched by motion away from the neutral position (note negative slopes). That is, PT, PB, and PL have abduction moment
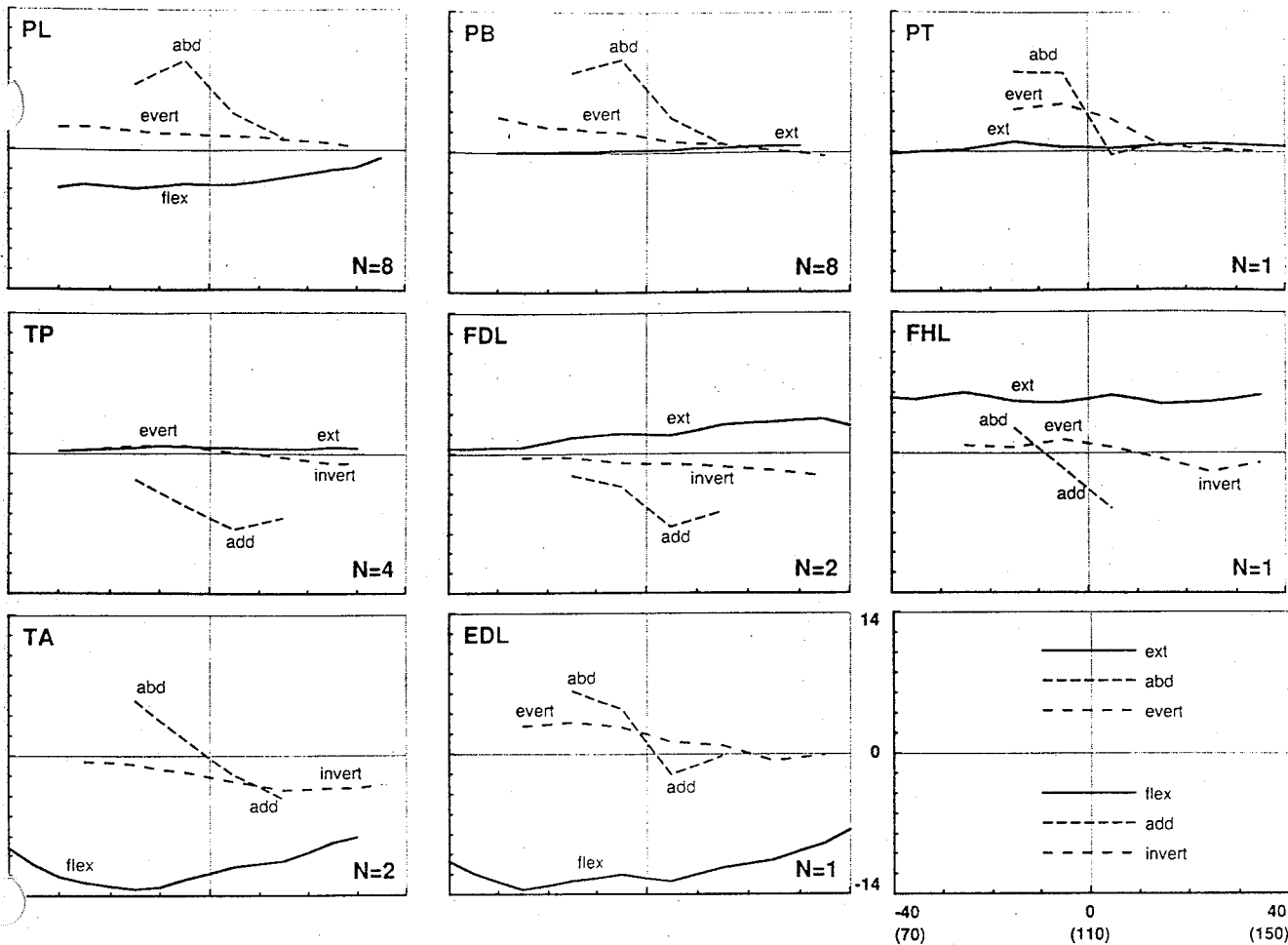
Fig. 4. For each muscle, the mean moment arm-joint angle relationships are plotted for all three anatomical axes. *N* denotes the number of animals included in each mean. Note that for these plots the *abbreviation beside each profile* refers to the action of that muscle while moment arms are either positive or negative (i.e., muscles with positive and negative moment arms in abduction are labeled as abductors and adductors, respectively). *abd*, abductor; *evert.* evertor; *flex*, flexor; *ext*, extensor; *add*, adductor; *invert.* invertor; muscle abbreviations as in Fig. 2

arms that are maximal when the ankle is adducted, and FDL, TP, and FHL have adduction moment arms that are maximal when the ankle is abducted. Muscles whose paths are confined relatively close to a midline between the malleoli (e.g., TA, EDL, see Fig. 2) tended to be lengthened by both abduction and adduction from neutral; they had abduction moment arms when the joint was adducted and adduction moment arms when the ankle was abducted (negative slopes crossing from upper left to lower right quadrants of Fig. 4). A slight tendency to similar "biactional" behavior was noted in the triceps surae, but the effect appears to be mechanically negligible, because the paths of these muscles lie nearly parallel to the shank instead of being restrained by retinacula close to the ankle joint like most other ankle muscles.

In eversion/inversion, moment arm-joint angle relationships were similar to those for abduction/adduction, but the magnitudes were generally much smaller. Muscles that had dominant abduction moment arms tended to be evertors, and muscles with adductor moment arms tended to be invertors. Moment arms were for the most part negligible for joint positions that shortened the muscles from their lengths at neutral joint position (lower left

and upper right quadrants of Fig. 4). This was also observed for muscles with biactional moment arms in abduction/adduction (TA, EDL).

The moment arms depend not only on the joint angle in the axis of the moment arm but also on the position of the joint in the other axes. These dependencies are shown as surface plots in Fig. 5 (abduction moment arm vs abduction and extension joint angles) and Fig. 6 (eversion moment arm vs eversion and extension joint angles). Dual dependencies between eversion and abduction were not examined. For the sake of brevity, only those muscles whose moment arms were joint angle dependent about both axes will be described here. PB and PT had abduction moment arms that increased when the ankle was extended and decreased when the ankle was flexed (with respect to the neutral position), but only when adducted away from neutral. The generally large adduction moment arm of TP tended to decrease as the ankle was moved from flexion to extension, particularly when the ankle was not in the neutral adduction position (note trough in middle of surface plot TP in Fig. 5). TA had a relatively large moment arm in abduction, but only when the ankle was adducted away from neutral in a slightly
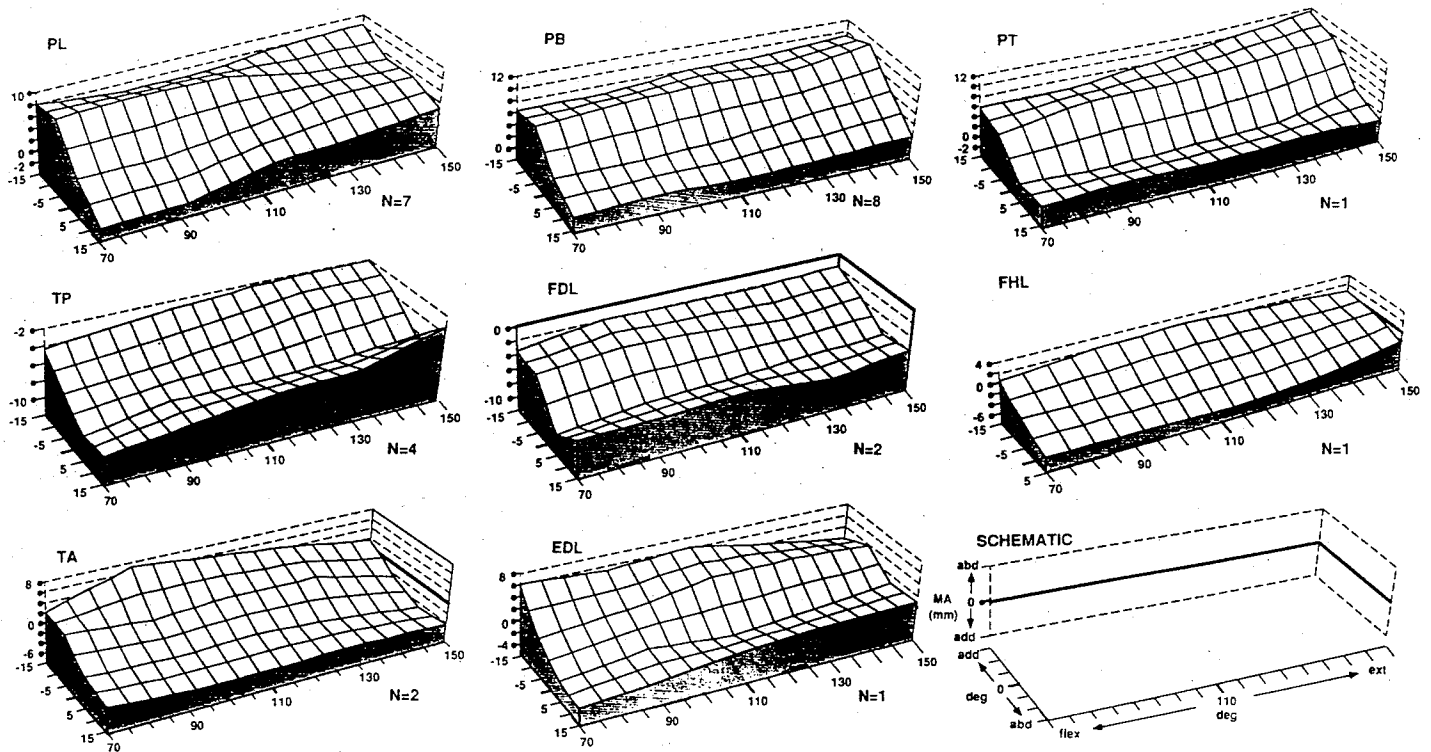
Fig. 5. Abduction moment arms (negative moment arms ⟹ adduction moment arms) are presented for the full range of motion for abduction/adduction at all flexion/extension joint positions. Moment arms were measured at the joint positions whose values are noted numerically on each axis, and intermediate values of the regular grids were linearly interpolated. Plots are grouped according to function: *row 1*, primary abductors; *row 2*, primary adductors; *row 3*, primary flexors with bidirectional abduction/adduction moment arms. All primary abductors along with extensor digitorum longus (EDL) and all primary adductors along with tibialis anterior (TA) also demonstrate eversion and inversion moment arms, respectively. Muscle abbreviations as in Fig. 2; other abbreviations as in Fig. 4

flexed position. Somewhat similarly, EDL had a broader range of abduction/adduction moment arms for flexed rather than extended ankle positions. In the eversion/inversion axis, PL demonstrated the largest interaction with the flexion/extension axis (Fig. 6), going from one of the largest everting moment arms when the ankle was inverted and flexed to essentially zero when everted and extended. EDL and TA had maximal eversion and inversion moment arms, respectively, for positions of slight ankle flexion (90°) and coincident inversion and eversion, respectively.

Interanimal variability

For most muscles, the moment arm profiles were consistent in all animals examined. The gross anatomical appearance of the ankle joint and related muscles and tendons was generally similar from animal to animal, but subtle differences in the position and laxity of retinacula were noted, usually after noting atypical moment arm profiles in one or more muscles (see Figs 7–9). When a muscle was observed to have an atypical moment arm profile about one or more axes, the moment arm of the same muscle on the contralateral leg was examined at least qualitatively. In general, we found that even these atypical muscles exhibited bilateral symmetry in a given animal. Variability between animals was most apparent for the moment arms in the nondominant axes. For example, PL always demonstrated its largest moment arms in abduction, but the secondary moment arm might be in eversion in some animals or in flexion for others (Fig. 7). This variability was also observed for PB (Fig. 8), which was always primarily an abductor but exhibited a wide range of action in eversion. The mean data for PB in extension/flexion include one significant outlier that may confuse the interpretation of this muscle's action. All other specimens had very slight extensor action over the entire range of motion, but this one had a large flexion moment arm, perhaps due to a shift in the retinacula or the center of rotation as a result of prior injury. TP (Fig. 9) showed more consistency, with only small, quantitative changes in absolute moment arms between specimens.

Interanimal variability of moment arms was greatest for tethered muscles (i.e., muscles whose path is constrained by soft tissue retinacula that prevent muscles from bow-stringing; e.g., PL, TA) whereas pulleyed muscles (i.e., muscles whose tendons ride over boney protuberances; e.g., FDL, PB, TP), typically, showed less variability. Muscles with straight paths from origin to insertion (e.g., triceps surae) had simple and consistent moment arms in our preliminary studies and so were studied in detail in only one or two preparations.
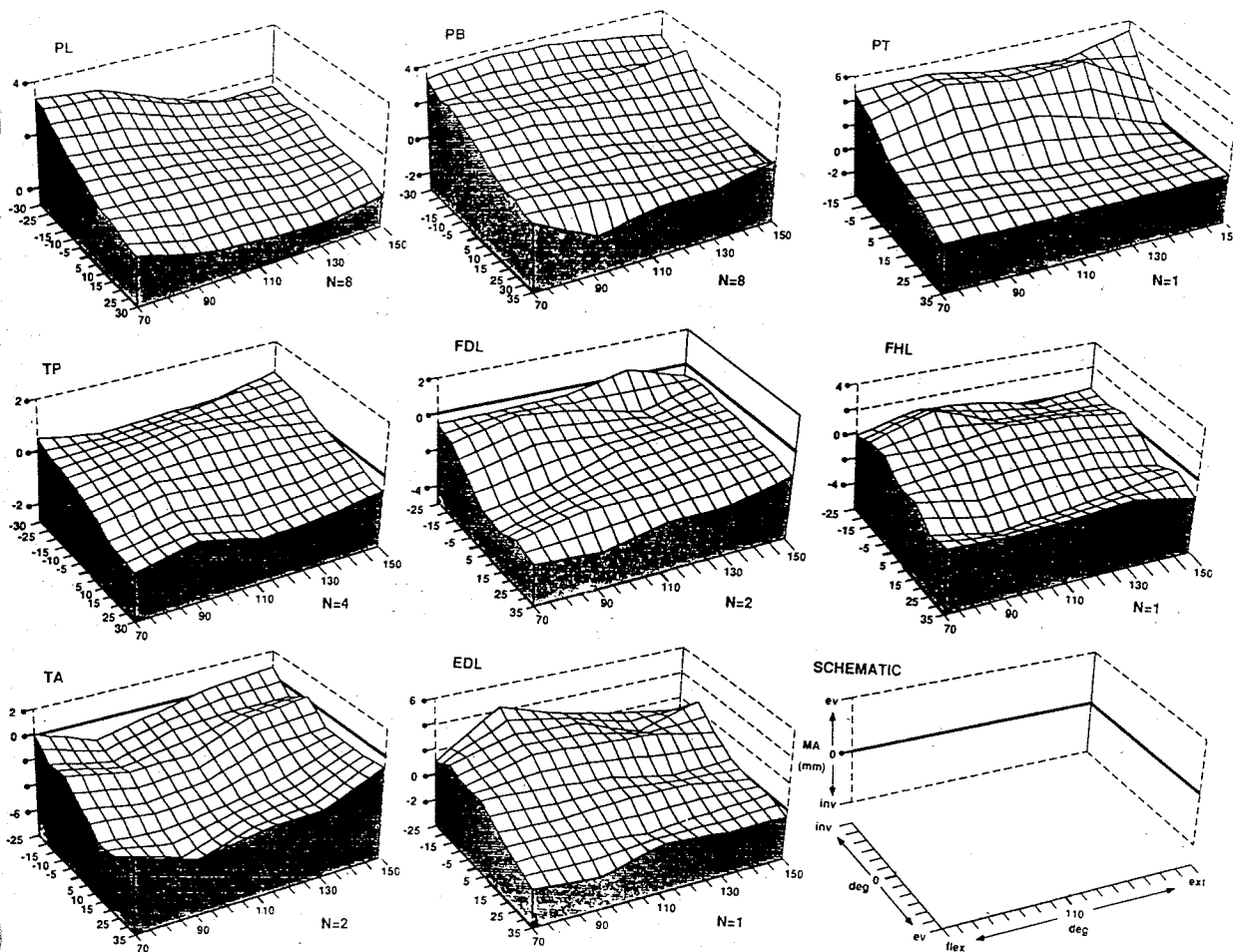
Fig. 6. Eversion moment arms (negative moment arms ⇒ inversion moment arms) are presented for the full range of motion for eversion/inversion at all flexion/extension joint positions. Moment arms were measured at the joint positions whose values are noted numerically on each axis, and intermediate values of the regular grids were linearly interpolated. Plots are grouped according to function: *row*

1, primary abductors; *row* 2, primary adductors; *row* 3, primary flexors with bidirectional abduction/adduction moment arms. All primary abductors along with EDL and all primary adductors along with TA also demonstrated eversion and inversion moment arms, respectively. Abbreviations as in Figs 2 and 4

Working range

The ability of a muscle to perform work in a particular joint axis cannot be determined by moment arm alone, because the joint may have a restricted range of motion in that axis or because the moment arm may be large only for a small range of joint angles. Table 1 summarizes the total muscle length changes that could be produced over the anatomical range of motion in each axis. The simple sum for all axes given in the last column provides an estimate of the largest possible range of muscle lengths that might be encountered over all joint angles; the actual anatomical range may be slightly smaller because of the complex interaxis dependencies, shown in Figs 5 and 6.

Discussion

Primary actions

Given the moment arm data reported here, it is possible to group the feline ankle muscles by their primary ac-

tions. The main flexors of the ankle are TA and EDL, which also aid in abduction/adduction and in inversion and eversion, respectively. SO (plus the gastrocnemii and plantaris) dominate extension (see Young et al. 1992). Although FHL has an extensor moment arm that is only a third that of SO, nevertheless it is likely a major ankle extensor, owing to its relatively large physiological cross-sectional area (Sacks and Roy 1982). PB, PT, and PL are primarily abductors, but also evertors, when the muscles are lengthened by inverting the joint. PL is also a modest flexor, but only when the ankle is flexed with respect to the neutral position. FDL and TP are primarily adductors (aided by FHL), but also invertors, when the muscles are lengthened by everting the joint. FDL is also a modest extensor, but only when the ankle is extended with respect to neutral.

For both eversion/inversion and abduction/adduction, the moment arms of the ankle muscles generally exhibit strong joint angle dependencies that may contribute to the intrinsic stability of the ankle in these axes (see below and Young et al. 1992). That is because these moment arms for each muscle tend to become larger when the joint is moved away from neutral in a direction
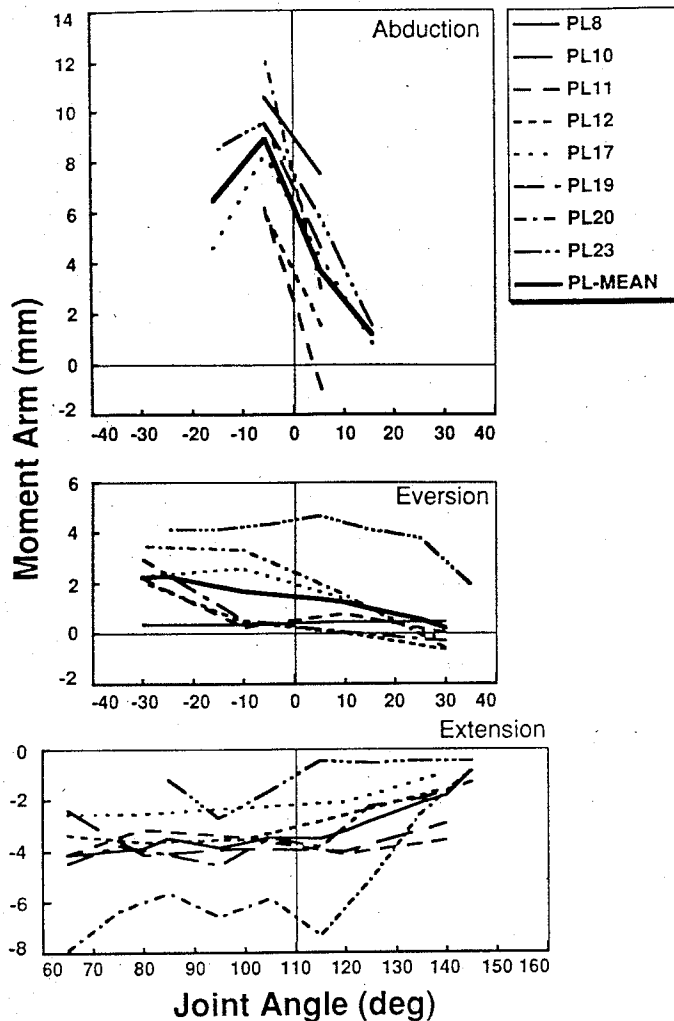
Fig. 7. Individual moment arm-joint angle relationships along with the mean profile (i.e., averaged across animals) are presented for peroneus longus (PL) about each anatomical degree of freedom, with the other two axes fixed in their neutral positions (abduction/adduction = 0, eversion/inversion = 0, flexion/extension = 110). For each plot, the direction noted refers to both positive moment arm and positive joint displacement away from the neutral position. In all cats PL had primary moment arms in abduction, but considerable interanimal variability was observed with respect to secondary moment arms
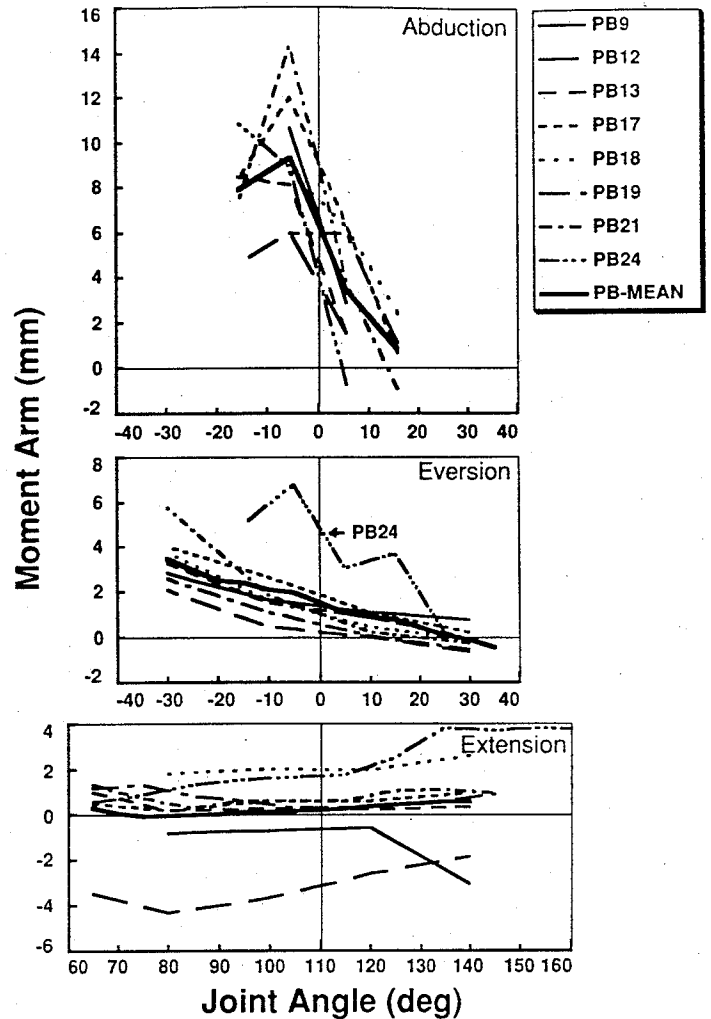
Fig. 8. Individual moment arm-joint angle relationships along with the mean profile (i.e., averaged across animals) are presented for peroneus brevis (PB) about each anatomical degree of freedom, with the other two axes fixed in their neutral positions (abduction/adduction = 0, eversion/inversion = 0, flexion/extension = 110). For each plot, the direction noted refers to both positive moment arm and positive joint displacement away from the neutral position. Of particular note is the fact that PB24 demonstrated relatively large eversion moment arms, in comparison with those of other animals. See Results for an explanation of the unusual flexion moment arm for PB13

that elongates the muscle. Thus, these muscles are particularly effective at pulling the joint back toward neutral, but not in deflecting it away from neutral.

The general tendency to have large moment arms in extension/flexion, intermediate moment arms in abduction/adduction, and relatively small moment arms in eversion/inversion may correspond to the magnitude of the torques that would generally be expected in these axes at the ankle. Extension/flexion is, of course, the axis for supporting body weight and for rapid acceleration of the foot to clear the ground in the swing phase of locomotion. Abduction/adduction would correspond to lateral forces that would mostly be applied to or by the ball of the foot (e.g., in the platform perturbation paradigm used by Macpherson et al. 1988a;b), which provides a relatively long lever arm (about 6 cm) for the generation of ab-

duction/adduction torque at the ankle. The largest loads in eversion/inversion would probably occur during rocking of the foot during weight bearing to shift the center of pressure from the center to the lateral edges. The effective lever arm that transmits these forces to produce torque at the ankle is half the width of the foot, which is only about 2 cm. In attempting to relate these presumptive functions to observable behavior in the cat, it is worth reemphasizing the steep angle-dependency of the muscle moment arms. These suggest that the cat can effectively level and center its foot following external perturbations, but that it may have relatively little ability voluntarily to deflect its foot away from these neutral positions in the absence of external forces.
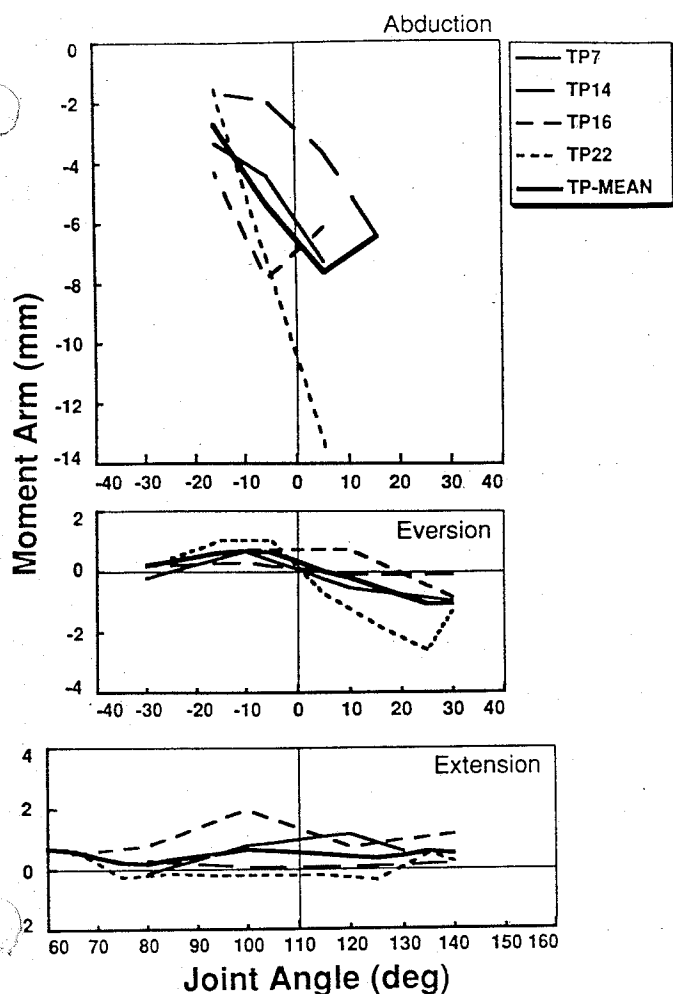
Fig. 9. Individual moment arm-joint angle relationships along with the mean profile (i.e., averaged across animals) are presented for tibialis posterior (*TP*) about each anatomical degree of freedom, with the other two axes fixed in their neutral positions (abduction/adduction = 0, eversion/inversion = 0, flexion/extension = 110). For each plot, the direction noted refers to both positive moment arm and positive joint displacement away from the neutral position. For all cats examined, moment arms about the eversion and extension axes were very small and relatively invariant (in contrast to peroneus longus and peroneus brevis; see Figs 7,8). TP always had its largest moment arm in adduction

Interpretation of EMG studies

In view of the present findings, previous studies (Abraham and Loeb 1985; Abraham et al. 1985; O'Donovan et al. 1982, 1985) that examined the use of the distal hindlimb musculature during normal and perturbed gait appear to have misinterpreted the function of some of these muscles. Those studies apparently based their interpretation of musculature function on two erroneous assumptions:

1. That muscles crossing the ankle just posterior to the malleoli (the presumed center of rotation in extension/flexion, see Fig. 2) are plantar flexors;
2. That the feline ankle (like the human ankle) has only two mechanical degrees of freedom, restricted to extension/flexion and eversion/inversion.

It now appears that many of the muscles that pass close to and around the malleoli have negligible moment arms in extension/flexion and, at most, modest actions in eversion/inversion. Instead, they exert large torques and undergo large length changes for motion in abduction/adduction, for which there are very little kinematic data available. In all cases, these moment arms become larger when the muscles are stretched, a condition that will also increase the force output of the muscle as a consequence of the force/length and force/velocity properties of muscle. The torque at the joint is the product of muscle force and moment arm, suggesting that these muscles would provide joint stability intrinsically (i.e., without requiring any change in neural drive) if they were cocontracted (Young et al. 1992). Such activity has been observed for some of these muscles; for example, PB and TP are coactivated during the stance phase of walking (Abraham and Loeb 1985; O'Donovan et al. 1982). FDL and EDL are active during different parts of the swing phase, but these two muscles show "facultative" recruitment during stance phase that is quite variable from animal to animal and tends to increase with gait speed (Loeb 1993). FDL and PL have nearly reciprocal actions in all three axes; their consistent cocontraction during the flexion phase of swing would tend to bring the foot to neutral abduction/adduction and eversion/inversion even if it wound up in a deviated orientation during push-off.

Previous studies (cf. Abraham and Loeb 1985; O'Donovan et al. 1982) have assumed that FHL and FDL are anatomical synergists because of their common tendon of insertion and partially common origin on the tibia. This assumption lead to an apparent paradox, because their recruitment patterns during locomotion are quite different. Examination of the ankle cross section (see Fig. 2) suggest that these muscles have minimal synergistic capabilities at the ankle, a notion supported by the moment arm data reported here. However, clearly these muscles are toe flexor synergists. During the stance phase of gait, large plantarward forces are required at the ankle and, particularly in late stance, at the toes. FHL is well suited to assist the triceps surae because of its large PCSA and ankle-extensor moment arm. Shortening of this muscle during extension at the ankle will be largely offset by dorsiflexion of the toes in late stance, permitting the muscle to work more efficiently under near-isometric conditions. FDL probably flexes the toes and stabilizes the ankle (as noted above) during swing phase, when its negligible extensor moment would not interfere with dorsiflexion of the ankle. The occasional cocontraction of FDL and FHL during jumping, scratching, and paw-shaking (Abraham and Loeb 1985) may be related to the coincidental need for their various, different actions at the ankle instead of, or in addition to, their synergistic role in protruding the claws.

The interanimal variability in moment arms observed in this study (most noticeably for muscles tethered close to the joint center) suggests caution in pooling functional data among different specimens, a common practice in kinesiological and neurophysiological studies. Apparently idiosyncratic differences between animals have been noted for kinematics (for paw-shaking in cats; Hoy and
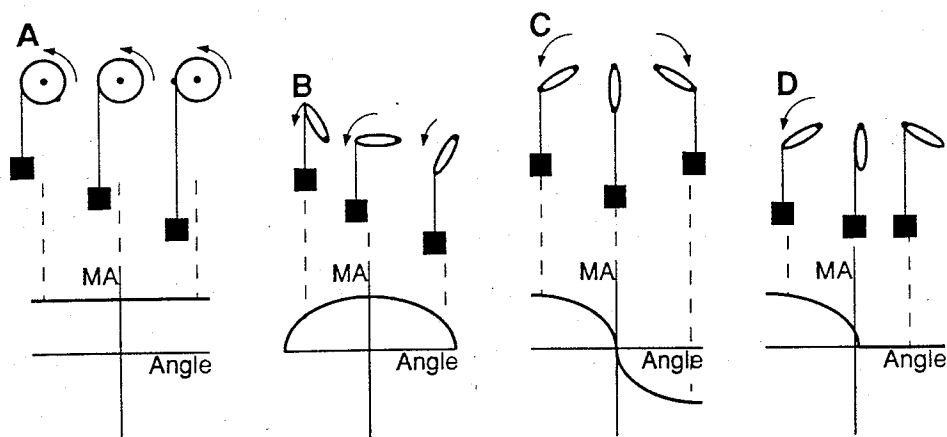
Fig. 10A–D. A schematic demonstration of the variety of typical moment arm-joint angle relationships that were observed in this study along with examples of the sorts of mechanical constraints on tendon path that can give rise to such relationships. **A** A simple agonist has its path constrained by a pulley, thus resulting in relatively constant moment arms (*MA*) for all joint positions (e.g., flexion/extension moment arms for flexor hallucis longus). **B** A complex agonist has a quasi-sinusoidal moment arm-joint angle relationship which may be the result of either an unconstrained path (e.g., flexion/extension moment arms for soleus) or a tethered path (e.g., flexion/extension moment arms for tibialis anterior, TA, and extensor digitorum longus, EDL). The curvature of this relationship will be defined by the relative distances of the tethers or attachments from the joint center and segment midlines. **C** Bidirectional stabilizing moment arms are observed for unconstrained and tethered muscles when the joint is moved perpendicular about an axis such that any motion away from midline produces muscle lengthening (e.g., abduction/adduction moment arms for TA and EDL). **D** Unidirectional stabilizing moment arms may result from either a polycentric joint or a tendon path constrained to pass around a strut (e.g., peroneus brevis and peroneus tertius)

Zernicke 1986; Smith et al. 1980) and EMG during locomotion and cutaneous reflexes (Loeb 1993). Unfortunately, it is not feasible to perform a systematic study of the joint mechanics in a given specimen for all of the muscles that are involved in the behavior under study. Until efficient and sufficient screening tests are devised, it will be difficult to decide whether behavioral and physiological variability is a direct consequence of anatomical variability or the result of other, more complex developmental and experiential factors.

Mechanical analogues of joint actions

It may be useful conceptually to consider the types of mechanical structures that can give rise to the various joint angle dependencies noted for the moment arms of the ankle muscles. If the center of rotation of a joint is not fixed with respect to the anatomical constraints on the path of the tendons (as in the polycentric rotation of the human knee; Smidt 1973; Soudan et al. 1979), then virtually any complex pattern may arise. However, Fig. 10 shows a family of planar, unicentric mechanisms that can replicate virtually all of the moment arm-joint angle relationships reported here for the various ankle muscles in the various axes of rotation. This is not to suggest that any of these particular cam and lever mechanisms is actually embodied in the ankle joint, but only to consider the range of structure-function relationships that might occur. In principle, it should be possible to locate the instantaneous center of rotation in each axis by triangulation of the moment arms from the anatomical paths of the tendons of the various muscles. In practice, this would be both computationally and experimentally diffi-

cult because it would require a complete and accurate set of anatomical coordinates and moment arm functions from several muscles in a single preparation.

Principles of musculoskeletal architecture

Mammalian muscles show a striking range of architectural variability at the levels of fascicular organization and musculoskeletal action, yet they are all composed of the same fundamental contractile unit, the sarcomere. The force-generating and thermodynamic properties of sarcomeres are strongly influenced by the range and rate of length changes imposed upon them, resulting in a relatively narrow range of conditions under which they can produce maximal or economical work or force. This has tempted many authors to speculate that some developmental process constrains the fascicular and musculoskeletal architectural patterns to be complementary to each other so that the sarcomeres generally work under similar kinematic conditions in all muscles (Gans and Bock 1965; Gans and Gaunt 1991; Goslow et al. 1977; Otten 1987).

In fact, we came to make the observations reported here because of faith in this teleological principle. Initially, our mechanical goniometer permitted motion only in extension/flexion and eversion/inversion, which resulted in data suggesting that the entire range of motion in muscles such as TP and PB would be only 10–20% of their fascicle lengths. As Table 1 shows, the range of fascicle length changes that can occur over the full anatomical range of motion at the ankle is a fairly consistent 50–100% of normalized fascicle length for all of the muscles that we examined (column FS for fascicle stroke), despite

the much greater range of both fascicle lengths and moment arms. The range of length changes under which these muscles normally perform active mechanical work may be even more closely regulated as a result of simultaneous motion across other joints crossed by some of these muscles (e.g., EDL, FDL, FHL, and PT) and selective recruitment in different phases of a given behavior. These data provide empirical support for the notion that there is a mechanical complementarity between the gross musculoskeletal architecture and the intramuscular fascicular architecture of mammalian muscles.

These data also lend insight into the function of FHL at the ankle joint. It has a mass similar to TA, but when examined superficially it appears much smaller because of its deep location and apparently flat superficial profile, compared with TA's round profile perched on top of EDL. Because FHL has much shorter fascicles than TA, it has a much larger physiological cross-sectional area (Sacks and Roy 1982) and, therefore, can generate 3–4 times as much force as TA. It can also generate 4–5 times as much force as SO. This, despite having an extensor moment arm that is only half that of SO and TA, FHL can actually generate a much larger ankle torque than either of those more recognized prime ankle movers.

Conclusions

The moment arm measurements reported here demonstrate that the mechanical structure of the feline ankle is more complex than was previously believed. This more accurate description of the actions of the various muscles should aid in the interpretation of both their patterns of use and their patterns of reciprocal and nonreciprocal heteronymous reflexes (Nichols 1989). It is also a challenge to theoreticians and modelers, who must simplify these empirical descriptions into more abstract entities that still capture their salient biomechanical features.

References

Abraham LD, Loeb GE (1985) The distal hindlimb musculature of the cat. Patterns of normal use. Exp Brain Res 58:580–593
Abraham LD, Marks WB, Loeb GE (1985) The distal hindlimb musculature of the cat. Cutaneous reflexes during locomotion. Exp Brain Res 58:594–603
An KN, Ueba Y, Chao EY, Cooney WP, Linscheid RL (1983) Tendon excursion and moment arm of index finger muscles. J Biomech 16:419–425
An KN, Takahashi K, Harrigan TP, Chao EY (1984) Determination of muscle orientations and moment arms. J Biomech Eng 106:280–282
Crouch JE (1969) Text-atlas of cat anatomy. Lea and Febiger. Philadelphia
Gans C, Bock WJ (1965) The functional significance of muscle architecture – a theoretical analysis. Ergeb Anat Entwicklungsgesch 38:116–141
Gans C, Gaunt AS (1991) Muscle architecture in relation to function. J Biomech 24:53–65
Goslow GE Jr, Reinking RM, Stuart DG (1973b) Physiological extent, range and rate of muscle stretch for soleus, medial gastrocnemius and tibialis anterior in the cat. Pflugers Arch 344:77–86
Goslow GE Jr, Cameron WE, Stuart DG (1977) Ankle flexor muscles in the cat: length-active tension and muscle unit properties as related to locomotion. J Morphol 153:23–38
Griffiths RI (1987) Ultrasound transit time gives direct measurement of muscle fibre length in vivo. J Neurosci Methods 21:159–165
Hoffer JA, Caputi AA, Pose IE, Griffiths RI (1989) Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. Prog Brain Res 80:75–85
Hoy MG, Zernicke RF (1986) The role of intersegmental dynamics during rapid limb oscillations. J Biomech 19:867–877
Levens AS, Inman VT, Blosser JA (1948) Transverse rotation of the segments of the lower extremity in locomotion. J Bone Joint Surg 30:859–872
Loeb GE (1993) The distal hindlimb musculature of the cat: interanimal variability of locomotor activity and cutaneous reflexes. Exp Brain Res 96:125–140
Macpherson J (1988a) Strategies that simplify the control of quadrupedal stance. I. Forces at the ground. J Neurophysiol 60:204–217
Macpherson J (1988b) Strategies that simplify the control of quadrupedal stance. II. Electromyographic activity. J Neurophysiol 60:218–231
Nichols TR (1989) The organization of heterogenic reflexes among muscles crossing the ankle joint in the decerebrate cat. J Physiol (Lond) 410:463–477
O'Donovan MJ, Pinter MJ, Dum RP, Burke RE (1982) Actions of FDL and FHL muscles in intact cats: functional dissociation between anatomical synergists. J Neurophysiol 47:1126–1143
O'Donovan MJ, Pinter MJ, Dum RP, Burke RE (1985) Kinesiological studies of self- and cross-reinnervated FDL and soleus muscles in freely moving cats. J Neurophysiol 54:852–866
Otten E (1987) Optimal design of vertebrate and insect sarcomeres. J Morphol 191:49–62
Sacks RD, Roy RR (1982) Architecture of the hind limb muscles of cats: functional significance. J Morphol 173:185–195
Smidt G (1973) Biomechanical analysis of knee flexion and extension. J Biomech 6:79–92
Smith JL, Betts B, Edgerton VR, Zernicke RF (1980) Rapid ankle extension during paw shakes: selective recruitment of fast ankle extensors. J Neurophysiol 43:612–620
Soudan K, Van Audekercke R, Martnes M (1979) Methods, difficulties and inaccuracies in the study of human joint kinematics and pathokinematics by the instant axis concept. Example: the knee joint. J Biomech 12:27–33
Spoor CW, Van Leeuwen JL (1992) Knee muscle moment arms from MRI and from tendon travel. J Biomech 25:201–206
Spoor CW, Van Leeuwen JL, Mesker CG, Titulear AF, Huson A (1990) Estimation instantaneous moment arms of lower-leg muscles. J Biomech 23:1247–1259
Young RP, Scott SH, Loeb GE (1992) Joint-angle-dependent moment arms of feline ankle muscles. An instrinsic mechanism to stabilize posture. Neurosci Lett 145:137–140