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An intrinsic mechanism to stabilize posture – joint-angle-dependent moment arms of the feline ankle muscles

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The neuromuscular system can use sensory feedback to regulate motion, but these feedback loops involve relatively long delays (50–100 ms) and may produce undesirable oscillations. However, stabilizing changes in muscle force can also be provided intrinsically (i.e. without feedback) by 2 properties of the muscle itself, its force-length and force-velocity relationships. We have discovered another intrinsically stabilizing mechanism in the musculoskeletal architecture of the cat ankle joint. Many of its muscles have their predominant moment arms about the adduction/abduction axis, with smaller moment arms for inversion/eversion and about the principal axis of motion, dorsiflexion/extension. The magnitudes of the moment arms in ab/adduction and in/eversion depend strongly on joint angle, increasing for positions away from neutral that lengthen the muscles. Thus, co-activation of agonist–antagonist pairs, known to occur in these muscles, would provide immediate stabilizing changes in torque when the ankle is perturbed away from neutral position.

The mechanical action of a muscle upon the skeleton depends on the torque that it produces about each joint that it crosses. These torques are the products of the contractile force generated in the muscle (active or passive) and its moment arm about the joint. Therefore, the net torque acting on a joint can be understood only if the moment arms of all relevant muscles are accurately known. Moment arm is defined as the shortest perpendicular distance from the line of pull of the muscle to the center-of-rotation of the joint. However, even in simple hinge joints (unicentric, single axis of motion), the moment arms are usually not constant over the range of motion. If the center-of-rotation of the joint changes as a function of joint angle or loading (i.e. the joint is multicentric rather than unicentric), or if the muscle path is constrained out of the plane(s) of motion by riding over boney prominences (pulleys) or through connective tissue sheaths (tethers), then the moment arms may have large and complex joint-angle dependencies that are difficult to determine from simple anatomical inspection [20].

It is possible to measure the instantaneous moment arm of a muscle about a particular axis by applying small rotations about that axis and measuring the resulting tendon motions [3, 4, 18, 19]. The moment arm (in mm) is simply the amount of tendon motion (in mm) divided by the change in joint angle (in radians). In contrast to geometrical estimates of moment arms, which require the location of the joint center and the muscle path about it to be known with certainty, this technique allows moment arms to be accurately measured without having to locate the joint center (though small errors may result if care is not taken to ensure that joint positions are accurately measured). However, to ensure that any joint motion results in the appropriate tendon motion, tendon slack should be removed and tendon tension should be similar for all joint positions. We used this technique to obtain precise moment arm data at multiple joint positions about each axis for a variety of feline ankle muscles. Two other techniques were then used to validate these moment arm measurements (see below).

In pentobarbital anesthetized cats (*Felis domesticus*), the muscle of interest was dissected free from the surrounding connective tissue. The muscle's origin, insertion, and tethers along with other muscles sharing its tethers were left intact and bathed in saline to avoid changes in its course that might affect its moment arms. We then used sonomicrometry [10, 11] to measure small changes in tendon position with respect to the tibia during small increments in ankle angle. Sonomicrometry (Sonomicrometer 120, Triton Technology, San Diego,

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CA) uses piezoelectric crystals to determine distance from acoustic transmission time, with the distance between the crystals (0.04 mm resolution) computed electronically as the product of transmission time and the velocity of sound. One piezoelectric crystal (acting as an ultrasound transmitter) was suspended from one of the bone screws that prevented motion of the tibia. The receiving crystal was attached to a thin silastic sheet (<6×8 mm), which was then sutured to the cord-like tendon (i.e. not aponeurosis) of the muscle of interest, such that it faced along the tendon (i.e. the direction of muscle pull). One experimenter was given the sole responsibility of carefully moving the joint through its range of motion and ensuring that the sonomicrometer had a strong, consistent piezoelectric signal. The foot was clamped to a tri-axial joint rotation apparatus (see Fig. 1), which allowed the joint to be moved in precise 10° increments about its 3 anatomical degrees of freedom: dorsiflexion/extension (rotation of the foot in the sagittal plane), inversion/eversion (rotation of the foot about its long axis), and abduction/adduction (rotation of the foot about the long axis of the leg). We took care that our clamps did not produce artifactual forces that might sublux the joint. Tendon slack was removed by pulling on the proximal end of the tendon with a 200 g force. Moment arms were determined by recording the tendon motion that occurred during 2 successive 10° increments of joint position – 20° increments (typically) produced similar results – about 1 degree of freedom with the other 2 axes fixed in their neutral positions; for extension/flexion, neutral was 110 degrees, the functional standing angle [9].

Moment arm measurements were validated by examining the mechanical advantage of the tendon about the joint center during both passive and active muscle force, at each flexion/extension joint position (abduction/adduction and inversion/eversion axes were restricted to neutral angles). For these validations, the foot was clamped to a strain-gage apparatus, which measured a composite ankle torque (flexion/extension torque and inversion/eversion torque). The first validation technique involved examining the mechanical advantage (i.e. moment arm) of the muscle about the joint center required to produce joint torques (i.e. strain-gage deflection at a known distance from the joint center) during the application of known forces (200 g and 400 g) to the tendon.

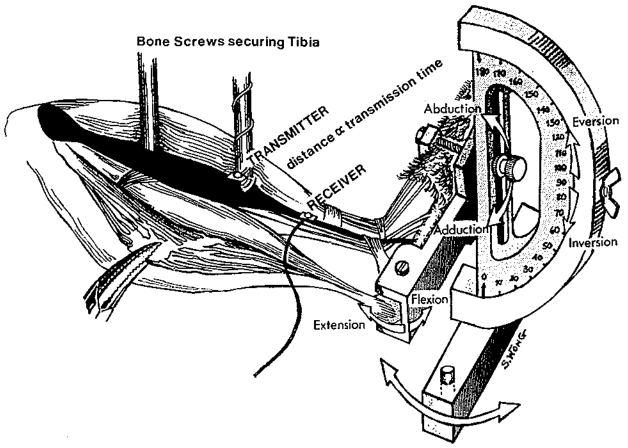

Fig. 1. Apparatus used to determine moment arms. Sonomicrometry [10, 11] was used to measure tendon motion during small increments in ankle angle (see text) about all 3 anatomical axes. Moment arms were then determined for each anatomical axis.

For the second validation technique, tendon motion was examined during tetanic stimulation (4 times threshold) of the nerve branch innervating the muscle of interest. Tendon motion was again measured, along with ankle torque and any changes in the length of the muscle fascicle and an exposed tendon section. These latter 2 measurements were made so that variations in these measurements could be removed from tendon displacement measures. Functional moment arms during active stimulation were then determined using the tendon displacement method and mechanical advantage of the tendon about the joint (using the passive tendon force/joint torque relationships produced by the other validation technique). Although all techniques produced similar moment arm estimates, small differences were observed across the various techniques. However, it should be noted that both validation techniques are hypersensitive to errors (or fluctuations) in the magnitude of active and passive force application, respectively.

Initially, we assumed that the feline ankle joint had only the 2 degrees of freedom for which muscle actions have been described, extension/flexion and inversion/eversion [1, 6]. Therefore, we were surprised to find several muscles with very small moment arms about both these axes (see TP, PB, FDL in Fig. 2B,C), suggesting that they would produce minimal torque. Alexander [2] noted that muscles with short moment arms usually have a highly pinnate arrangement of relatively short muscle fibers, thus magnifying any changes in fiber length. However, the muscles in question are not strikingly more pinnate than other muscles with large moment arms in flexion/extension [17]. This apparent contradiction was resolved by noting that the ankle joint of the cat moves easily over a ±15–25° range in ab/adduction and about this axis, these muscles have surprisingly large moment arms (Fig. 2A). Similar data were obtained when the foot was clamped only around the metatarsals or with an additional screw into the calcaneus. In the human ankle joint, in contrast, ab/adduction of the foot occurs predominantly as rotation of the tibia [14], which we clamped rigidly in these experiments.

The plots of moment arm vs. joint angle in Fig. 2 show

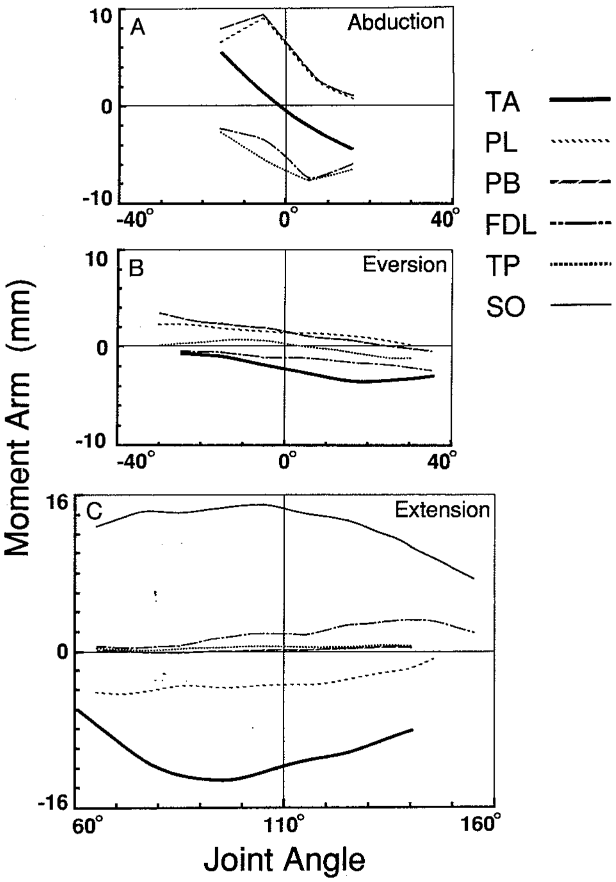

Fig. 2. Moment arm data (means of 2–7 specimens) are presented for all 3 anatomical axes (identical scales; positive refers to increasing angle and torque in the direction indicated on each graph) for 5 muscles studied in detail: tibialis anterior (TA), peroneus longus (PL), peroneus brevis (PB), flexor digitorum longus (FDL), and tibialis posterior (TP), plus soleus (SO) in flexion/extension. In ad/abduction (A), the absolute values of the moment arms increase as all muscles lengthen and decrease as they shorten. In in/eversion (B), trends similar to those in ad/abduction were observed, though moment arms were generally smaller. In flexion/extension (C), some muscles had small moment arms (or positive rather than the negative slopes seen in ad/abduction and in/eversion) in comparison to the large moment arms of a major extensor (SO) and flexor (TA), which were maximal at mid-range joint angles.

2 types of relationships. Plots from muscles that have large moment arms in extension/flexion (e.g. soleus and tibialis anterior), tend to be horizontal, with broad maxima near mid-position, consistent with the quasi-sinusoidal relationship expected for an unconstrained, coplanar muscle acting upon a simple hinge-joint [7]. In contrast, moment-arm plots for ad/abduction and in/eversion tend to have negative slopes. The upper left and lower right quadrants of these plots both represent regions where increasingly eccentric joint angles cause increasing increments of stretch in the muscles because of increasing moment arms. Thus, for a given amount of force in such a muscle, the torque on the joint would be large when that muscle was working to pull the foot back to mid-position (neutral) in that axis and much smaller if the foot was already deviated from neutral in the direction toward which the muscle pulls. For tibialis anterior, a major dorsiflexor, the moment arm in ad/abduction actually reverses sign so that tension in the muscle tends to pull the foot back towards neutral when the ankle is either abducted or adducted. Such dependencies complicate the interpretation of isometric forces at the foot that have been measured following electrical stimulation of some of these muscles in a single position [13].

Although for some muscles considerable inter-animal variability was observed in the magnitudes of the various moment arms (most noticeably for a muscle's non-primary axes), slopes of the curves were similar in all animals. That is, across all cats, the primary moment arm for a particular muscle was always about the same axis, but some muscles demonstrated secondary moment arms about either one or the other of the non-primary axes, depending on the individual animal. Inter-animal moment-arm variability was greater for tethered muscles than for pulleyed muscles.

One motor strategy for maintaining a desired joint position is cocontraction of antagonist pairs of muscles. Even in the absence of reflexes, such a system would tend to oppose perturbations because of the spring-like (length-tension) and dashpot-like (force-velocity) properties of muscle [12], which result in increased force in a stretched muscle and decreased force in a shortened muscle. During the stance phase of locomotion in the cat, cocontraction has been noted in ankle muscles acting in ad/abduction and in/eversion (but not flexion/extension) [1]. In response to a perturbation, the net restorative torque would be much larger than that predicted from the force changes in the muscles alone because these force changes are multiplied by similarly changing moment arms. In experiments where lateral perturbations were applied to the foot of the standing cat, large and immediate opposing ground reaction forces were measured [15, 16]. Given the unexpected mobility of the feline ankle in ad/abduction, these forces most likely resulted from large and immediate torque changes generated by already active musculature rather than passive properties of ankle ligaments.

The complex articulating surfaces and ligaments of the ankle suggest that its motion may be multicentric in one or more axes under normal loading conditions. However, multicentricity is neither a necessary nor a sufficient condition for the stabilizing moment arms described here. In the feline ankle, the phenomenon depends on both joint geometry and the mechanical constraints imposed on tendon paths by retinacula near the medial and lateral malleoli, which act as struts to provide large moment arms in the horizontal plane. A similar effect may underlie small changes in moment arms noted in the human wrist for ulnar/radial deviation [5]. In contrast, the geometry of the human metacarpophalangeal joint results in moment arm curves with a positive, destabilizing slope (particularly for intrinsic muscles of the hand [4]). The stabilizing geometry described here may be expected in other joints with constrained tendons and in species other than the domestic cat.

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