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Short-Term Effect of Crural Fasciotomy on Kinematic Variability and Propulsion During Level Locomotion

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Abstract

Treadmill locomotion can be characterized by consistent step-to-step kinematics despite the redundant degrees of freedom. The authors investigated the effect of disrupting the crural fascia in decerebrate cats to determine if the crural fascia contributed to kinematic variability and propulsion in the limb. Crural fasciotomy resulted in statistically significant decreases in velocity and acceleration in the joint angles during level walking, before, during, and after paw-off, particularly at the ankle. A further finding was an increase in variance of the limb segment trajectories in the frontal plane. The crural fascia therefore provides force transmission and reduction in kinematic variability to the limb during locomotion.

Keywords

crural fascia; locomotion; propulsion; stability

Fascia is a pervasive tissue that connects and compartmentalizes muscle groups, thereby affecting the manner in which forces are transmitted and distributed throughout the limb (Garfin et al., 1981; Maas, Meijer, & Huijing, 2005). Anatomical studies (Stecco et al., 2008; van der Wal, 2009) have shown that the musculoskeletal system contains nested and interconnected soft tissues that envelope muscles and their compartments, and in turn link muscles in series and parallel combinations to bone. Through this network of connective tissue, including fascia, (sometimes referred to as anatomical trains) muscles transmit tensile force to the skeleton (Myers, 2009). In short, the musculoskeletal system constitutes a tensegrity network (Silva, Fonseca, & Turvey, 2010). Fascia in particular has been suggested to play roles in force transmission (Carrasco & English, 1999; Maas & Huijing,

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2005) and in sensory feedback, thus contributing to a substrate for motor control in partnership with the central nervous system (Silva et al., 2010; Turvey, 2007).

The hindlimb of the cat is composed of several limb segments that have muscular and connective tissue linkages allowing for multiarticular force transmission. One such connective tissue is the crural fascia, located in the posterior, distal hindlimb of the cat and the human. This fascia in the cat hindlimb surrounds the gastrocnemius muscles, originating proximally from the distal hamstrings (posterior biceps femoris and semitendinosus muscles) and inserting onto the calcaneus thereby linking the thigh and shank segments. Both the hamstrings and the gastrocnemius muscles are considered to provide propulsive force during movements such as walking (Prilutsky, Herzog, & Allinger, 1996; Rossignol, 1996) or jumping (Abraham & Loeb, 1985; Zajac, 1985). The gastrocnemius muscles contribute to propulsion through plantarflexion of the ankle and flexion of the knee. The hamstrings muscles are thought to contribute through hip extension and knee flexion by their conventionally defined attachments, and through plantarflexion at the ankle through the crural fascia (van Ingen Schenau, 1994). It is in fact possible to utilize the tendinous bands of the crural fascia to apply controlled length changes to the distal hamstrings muscles to investigate the proprioceptive pathways associated with these muscles (Hyde, Burkholder, & Nichols, 1999). These findings suggest that the crural fascia may be used to transmit propulsive force or alter stiffness across multiple joints in the cat hindlimb during locomotion.

The close anatomical association of the gastrocnemius muscles to the crural fascia suggests that this structure can also participate in elastic energy storage at the ankle. The gastrocnemius muscle heads are located deep to the crural fascia. These muscles connect to the calcaneus by way of an aponeurosis that can store elastic potential energy (Lichtwark & Wilson, 2006). Azizi and Roberts (2009) showed an underestimation of potential elastic energy storage if the perpendicular strain exerted upon the aponeurosis during muscle contraction is not considered. This suggests that an additional connective tissue structure can contribute to elastic energy storage. Given that the crural fascia surrounds the gastrocnemius muscles, it has the potential to experience perpendicular strain similar to the aponeurosis and act as an additional conduit of elastic energy strain.

It has been suggested that the crural fascia resists tensile loads in multiple directions given the bidirectional alignment of collagen fibers across the multiple layers (Stecco et al., 2009). Therefore the crural fascia may be acting as a bidirectional tensile element within the limb and this tensile property is capable of being altered by the activation level of muscles (Silva et al., 2010). During locomotion and other motor activities, forces due to active muscular contraction are distributed through tendon and fascia to exert stress on the skeleton, forming the tensegrity network. This network helps to coordinate and limit the kinematic degrees of freedom of the musculoskeletal system during activity. Under these conditions, the network responds globally to mechanical disturbances (Silva et al., 2010) and mediates energy dissipation (Hogan & Sternad, 2013). It can therefore be hypothesized that the tensegrity network can contribute to consistent kinematic trajectories during locomotion.

To address the functional implications of the crural fascia for force transmission and reducing kinematic variance during locomotion, we evaluated the kinematics of the hindlimb of the cat during level walking in both the sagittal and nonsagittal planes. We hypothesized that the crural fascia in the cat hindlimb would contribute to propulsive force transmission and act to maintain kinematic invariance of the limb trajectory during level walking. To test this hypothesis, we used a decerebrate preparation that exhibits natural stepping patterns on a moving treadmill. This approach allowed us to evaluate the contributions of fascia without the problems associated with surgical recovery. We found that fasciotomy led to a reduction in accelerations at the knee and ankle joints, and unexpectedly increased the variance of the limb segments.

Methods

Surgical Preparation

The effects of crural fasciotomy were investigated in six decerebrate cats walking at 0.7 m/s atop a treadmill. All experimental protocols were approved by the Emory University and Georgia Institute of Technology Institutional Animal Care and Use Committees.

For each experiment, the animal was initially anesthetized using isoflurane gas. An intravenous line with Ringer’s solution was inserted and sutured into the external jugular in order to administer fluids throughout the experiment. While under anesthetic the skin over the gastrocnemius muscle in the right limb was longitudinally split from the popliteal fat pad behind the knee to within 1 cm of the calcaneus. The skin was very carefully blunt dissected off the crural fascia and resealed using a flat-edged alligator clip.

The animal was then supported atop a variable speed treadmill in a natural stance by affixing the head to a stereotaxic frame and supporting the animal using a clamp applied to the base of the tail. The tail clamp was affixed to the side of the treadmill and adjusted once the animal was standing to allow for weight support during stance and toe clearance during swing. By clamping the tail we did not directly restrain the pelvis and therefore allowed for limited movement of the pelvis and hip. A premamillary decerebration was performed where the brainstem was transected at a 45° angle beginning rostral to the superior colliculi and ending rostral to the mammillary bodies allowing for the preservation of the sub thalamic nucleus. All brain matter rostral and lateral to the transection was removed. Kinematic markers were taped to the right hindlimbs (further described in the Kinematics section). The anesthetic was then slowly reduced until eliminated. Stepping was then evoked by either running the treadmill or occasionally with manual stimulation around the base of the tail. The tail height was then adjusted to ensure continuous paw contact with the treadmill during stance and clearance of the toe during swing.

Recordings were made under two conditions: (a) intact: no manipulations to the crural fascia and (b) fasciotomy: the crural fascia was longitudinally split and then horizontally transected through the medial and lateral bands (Figure 1C). Attempts were made to reverse the disruptions but the crural fascia did not remain re-attached once the animal began locomoting. After the fasciotomy, the skin was resealed with the alligator clip. A minimum of three trials was then recorded; a trial is defined as a consistent, spontaneous period of walking for at least 20 s. In some cases, the fasciotomy was performed in stages (longitudinal split, medial band transection, then lateral band transection), with trials collected after each stage. The data reported here were collected after the final stage of disruption. Trials were collected quickly in order to preclude any effects that may be attributed to fatigue. At the end of the experiment the animal was euthanized with 1 ml highly concentrated pentobarbital administered through the intravenous line, and a pneumothorax was performed.

Kinematics

The three-dimensional trajectories of reflective markers on the right hindlimb were used to describe the mechanical changes observed under different fascia disruption conditions. Kinematic markers were placed on the right limb at the iliac crest, greater trochanter, upper shank (to calculate the virtual knee), lateral malleolus, metatarsal phelangeal joint (MTP), and toe (Figure 1A). The virtual knee was calculated as a vector projection from the lateral malleolus marker though the upper shank. The magnitude of the vector was the measured length of the shank from the lateral malleolus to the center of the knee joint. Three-dimensional kinematics were recorded from the spontaneously stepping, premammillary cat using either two cameras with Peak Motus software (cat 4, 5, 6; Peak Motus 8, Peak Performance Inc., Denver, CO) which was later replaced with a six camera Vicon system (cat 1, 2, 3; Vicon Nexus, Vicon Motion Systems, Ltd., United Kingdom) at 125 Hz. Paw contact and paw-off were demarked post hoc by video analysis of the animal walking. Paw contact and paw-off were defined as the times when the toes initially make and lose contact with the treadmill respectively. This did not always coincide with maximal retraction and protraction of the limb. The data were analyzed using custom Matlab (The MathWorks, Natick, MA) scripts and each marker was low-pass filtered at 6 Hz. The resulting 3D marker traces were then used for all analyses presented in this article.

The joint angles of the hip, knee, and ankle (Figure 1A) were calculated as the included angle (the smaller of two angles between two segments) in order to investigate the relationship between the segments. Furthermore by differentiating the results twice we were able to calculate the angular accelerations of the joints. Each step was divided into 25 sections of equal time length, each representing 4% of the step cycle. This provided for equivalent time-length for each step allowing the angular, velocity, and acceleration trajectories for nine steps across three trials under each condition to be averaged together. Significant changes in the angles, velocities, and accelerations for all three joints were determined on a per animal basis using a *t* test ($\alpha = .05$). Four timepoints during the step cycle were selected: paw contact, at the point of maximum acceleration for each joint during stance, paw-off, and midswing. The results are summarized in Table 1.

During swing, the foot often moved laterally as well as anteriorly, a trajectory referred to as circumduction. At this time in the step cycle, the foot was not grounded by the treadmill and could therefore move freely in the transverse direction. To evaluate the change in circumduction of the paw during swing we calculated the circumduction area. This area is defined as horizontal movement of the MTP marker during swing for the duration of the step length. Due to slight medial-lateral variations in paw placement at the initiation and termination of swing the baseline of each step was adjusted so that the paw contact and paw-off were set to zero in the medialateral direction and the linear offset was used to adjust all additional swing points. The circumduction area was then calculated as the average under the curve for each step from the baseline-adjusted trajectory of the MTP during swing. The circumduction area from nine steps in each trial was evaluated and averaged together under each condition for each animal. The mean area and variance was then determined across all steps in a condition. A two-sample *t* test for unequal variances (in Matlab) was run on the circumduction area comparing the intact and fasciotomy areas ($\alpha = .05$). Bartlett's test was performed on the MTP area for each cat ($\alpha = .05$) to determine if the change in variance was statistically significant. Furthermore, the MTP kinematic marker allowed for the calculation of the duty factor. The duty factor was computed as the percent time in stance of each step. The mean value for each cat was compared using a paired samples *t* test.

Calculation of the segment angles provided a quantification of the orientation of the thigh (virtual knee to greater trochanter), shank (lateral malleolus to virtual knee) and foot (MTP to lateral malleolus) throughout the step cycle in the frontal and sagittal planes. The segment angles were calculated for five of the six cats as cat 6 lost the lateral malleolus marker during the split condition trials. The sagittal and frontal plane angles were calculated with the distal marker at the origin and the angle computed following Cartesian coordinates (Figure 1). The frontal plane segment angles were calculated as though looking at the cat from the front of the cat while the sagittal plane segment angles were calculated as though looking at the cat from the lateral side with the head toward the 0°. Nine consecutive steps from each trial were then normalized to 4% bins and averaged. Due to slight differences in base angle of trajectory of the segments in each trial in the same condition, all trajectories in a fasciotomy condition were averaged and the offset for each trial was then calculated. Each step in a trial was then adjusted by the corresponding offset value. This resulted in mean adjusted trajectories for each condition for each cat, thereby removing any bias in the variance calculation that could be attributed the trials in a condition not having the same mean. The angle at paw-off for intact compared to fasicotomy was selected for statistical comparison as it described the limb configuration at the beginning of swing, therefore providing insight initiation of circumduction and protraction of the limb. A *t* test for unequal variances was performed and significant was determined ($\alpha = .05$). The variance was calculated for each bin in the step cycle and then summed across the step cycle. Due to the large variability in summed variance results across cats we evaluated each segment in the frontal plane and did not include any data points that were at least two standard deviations above or below the mean of the points. This resulted in the satisfactory analysis of data from at least three cats. The same cats were used for both the frontal and sagittal plane analysis. We performed a two-sample *t* test for unequal variances on the summed variances to compare the intact and fasciotomy results ($\alpha = .05$).

An important methodological issue was the possibility that the effects we observed might have been due to deterioration of the preparation. This possibility was difficult to test due to the fact that fasciotomy was irreversible, despite numerous attempts to do so. In order to preclude this possibility, all trials were collected within an hour of the onset of locomotion even though most cats continued to walk for upwards of 4 hr. Following these measurements, the preparations were used for additional experiments, such as the removal of popliteal fat from the untreated limb (Falcon, Stahl, & Nichols, 2011). The success of these additional experiments indicated that the present results did not result from deterioration of the preparation (see Results section).

Results

Kinematic changes were observed following crural fasciotomy. We were confident that the observed changes resulted from the fasciotomy because we limited the time of observation to 1 hr. In addition, the untreated limbs of these animals were used to make additional measurements for other projects, with little sign of deterioration for 2–3 hr following the completion of the experiments reported here. For example, most of these animals were used to evaluate the influence of popliteal fat on acceleration, and it was found that acceleration increased following the manipulation (Falcon et al., 2011). Furthermore, in extensive studies of locomotion in premammillary decerebrate cats, useful data were acquired for up to 3 hr (Ross & Nichols, 2009). Finally, the fasciotomies were typically performed in stages, with progressive changes in kinematics at each stage, although only the results of complete fasciotomy are reported here. The above observations indicate that the alterations in kinematics resulted from the fasciotomy rather than changes in the state of the preparation.

Effects on Included Angles

There were modest but significant reductions in hip angle following fasciotomy, but no significant changes in knee or ankle position between the two conditions (Figure 2, Table 1). It is apparent from the position trajectories, however, that slopes of position versus time for the knee and ankle joints were lower during the latter stages of stance (E3). These changes in slope were reflected in significant changes in velocity and acceleration for the ankle and knee. In the following paragraphs we describe the general kinematics and detailed changes following fasciotomy at each joint.

The hip joint was initially flexed at paw contact and extended with increasing velocity and constant acceleration to approximately three quarters of the way through stance. The acceleration and velocity then decreased, slowing the joint down before the reversal in direction at paw-off. After paw-off, the hip was flexed through swing with decreasing velocity and decreasing acceleration to midswing when the velocity and acceleration began to increase. The acceleration peaked just prior to paw contact and began to decrease in preparation for the reversal of the direction of motion of the joint. Following crural fasciotomy, there was a trend for a decrease in hip velocity during late stance and midswing. Hip acceleration was also found to decrease during late stance and at paw-off, but these decreases were significant in only three of the animals. See Table 1 for further details.

The knee extended at paw contact, flexed through midstance as the center of mass passes over the limb, and then extended to paw-off to provide propulsion. The velocity and acceleration increased through the majority of stance peaking just prior to paw-off when maximum propulsive force is applied. The acceleration then decreased with a reversal in the direction of the joint toward flexion through mid-swing before extending to paw contact. The velocity and acceleration increased through the majority of swing peaking just prior to paw contact. As shown in Figure 2 and Table 1, after fasciotomy velocity (three animals) and acceleration (four animals) decreased significantly during late swing. Velocity also decreased significantly during early swing. Acceleration decreased at paw-off, but significantly in only one animal.

The ankle joint slightly extended at paw contact and flexed slightly as the center of mass passed over the joint and then extended to paw-off. The velocity and acceleration were constant for the first part of stance and then increased to just prior to paw contact. The velocity decreases for the first half of swing and then increases in the second half while the acceleration increases for the majority of swing. Both velocity and acceleration decrease prior to paw contact. Following fasciotomy, velocity decreased during late stance (significant in three animals) and early swing (significant in four animals). Acceleration decreased significantly during late stance and after paw-off in four animals.

In summary, there were significant and substantial decreases in velocity and acceleration during late stance and early swing for the knee and ankle joints. There was a trend toward similar decreases for the hip joint, but the effects of fasciotomy were clearly more marked at the two distal joints.

Effects on Limb Endpoint

Effects of crural fasciotomy on whole limb orientation during the step cycle were evaluated by measuring changes in the MTP trajectory in the horizontal plane. Figure 3A depicts the results from cat 6 for purposes of illustration. The horizontal trajectories of the MTP joint during swing before and after fasciotomy are shown in panels 3Aa and 3Ab. Panel 3Ac illustrates how the resulting circumduction area was calculated. Note that the trajectories are plotted on unequal axes (the medialateral axis has been amplified). There was a trend for an increase in circumduction area after fasciotomy in five of the six cats, although this trend did not reach significance. The mean and standard deviation of the area across all cats is depicted in Figure 3B where the mean area increased from 27.24 ± 12.6 cm^2 to 37.54 ± 29.6 cm^2. The increase in variance of the MTP trajectory across cats is depicted in Figure 3C. The mean variance increased from 160.03 ± 12.65 to 875.87 ± 29.59 as a result of the fasciotomy. The increase in variance of the circumduction area was statistically significant for each cat ($p < .000001$). Some medialateral movement was also noted during stance. The area enclosed by these trajectories did not change due to the linear paw contact with the treadmill, which grounded and limited the movement of the end point of the limb.

Although we saw changes in the variance of medialateral motion following fasciotomy, we did not observe a significant change in stride time or duty factor across all cats ($p > .26$).

Segment Angle Analysis

The previous analysis indicated that motion of the limb in the frontal plane would be affected by the fasciotomy to a greater extent than motion in the sagittal plane. In order to better understand how the different limb segments contributed to the altered movement patterns after fasciotomy, we analyzed the angles of these segments in world coordinates, referred to as segment angles.

Sagittal plane—The mean sagittal plane segment and limb angles did not change significantly after fasciotomy (Figure 4Ai). Both before and after fasciotomy, the limb was initially protracted at paw contact, became vertical by midstance, retracted to paw-off, and protracted through swing to paw contact. During limb protraction to paw contact the thigh and foot were protracting while the shank was nearly vertical. As stance progressed, the limb orientation angle and the thigh and foot segment angles increased toward vertical while the shank retracted toward the horizontal. During limb retraction to paw-off, the foot and thigh were also retracted while the shank remained in the nearly horizontal retracted position. During swing, the limb, thigh, and foot protracted to paw contact while the shank only began to protract in midswing returning to a near vertical configuration.

Mean frontal plane segment and limb angles—The frontal plane mean limb angle depicts the adduction of the limb throughout the step cycle, particularly at paw-off after fasciotomy. The frontal plane mean segment and limb angles showed increased adduction of the limb after fasciotomy (Figure 4). Although the limb segment trajectories varied in specific details across cats the general pattern was consistent across animals.

In the intact right hindlimb, the limb was initially abducted at paw contact. As the limb progressed to pawoff, the limb began to adduct, and the paw was moved more medial to the body. The limb then abducted through swing. After fasciotomy, the limb ($p < .014$ for three of five cats) increased in adduction, particularly at paw-off. The change in limb orientation can be attributed to changes in the shank and foot segments with minimal change occurring at the thigh segment. In one experiment we reduced weight support and then performed the fasciotomy in stages (data not shown). Under this condition of reduced weight support, the fasciotomized limb adducted to the point of physically interfering with the opposite limb, further indicating that the kinematic changes that were observed were due to the fasciotomy itself. Merely splitting the fascia longitudinally between the medial and lateral bands resulted in an immediate increase in medialateral motion.

Variance of limb segments across the step cycles—Upon fasciotomy, the segment and limb angles of the hindlimb exhibited greater variability in the frontal plane but remained relatively unchanged in the sagittal plane (Figure 5). Although the foot, thigh, and limb mean variances increased slightly in the sagittal plane, these increases were not statistically significant. The mean variance of the segment and limb angles in the frontal plane increased after crural fasciotomy. The shank and thigh segments were statistically significantly more variable across cats (*p*s = .004 and .015, respectively). One cat was removed from analysis as the mean variance of the segments were outlier points although this cat showed the same trend.

Discussion

Summary

We mechanically disrupted the crural fascia in order to investigate the role of this structure in the coordination of the right hindlimb of the spontaneously locomoting decerebrate cat during level walking. To fully describe the control of the hindlimb we examined horizontal, frontal, and sagittal plane kinematics. Although we found modest changes in the sagittal plane we surprisingly found increases in kinematic variance in the frontal plane. By completing the studies in the decerebrate preparation we were able to investigate the effects of fasciotomy immediately following the procedure, therefore avoiding any possible adaptations that might have occurred during surgical recovery in a chronically treated and otherwise intact animal. Our reduced preparation also precluded visual and vestibular inputs due to the level of transection and fixation of the head in the stereotaxic frame.

Effects of Fasciotomy on Coordination

Propulsion—The musculature of the limb provides for flexion and extension and the corresponding propulsive force during locomotion. The decreases in slope of the position trajectories for the knee and ankle joints and the associated decreases in velocity and acceleration indicate that the crural fascia plays an important role in the force transmission through the limb. The reduction in the maximum angular acceleration during stance after the fasciotomy suggests that there was a loss of torque at the joints (assuming a constant mass distribution) during late stance. Therefore the crural fascia acts to increase the torque at the knee joints and to some extent at the ankle by providing a greater moment arm at the joints given its connection from the hamstrings to the calcaneus. Furthermore, the significant loss of angular velocity during swing suggests that the crural fascia plays an important role in changing the limb direction even when the limb is not in contact with the ground.

During level walking, electromyographic recordings in the cat show (Rossignol, 1996) the activation patterns of the semitendinosus and posterior biceps femoris muscles have been shown to be more variable recordings at either or both paw contact and paw-off (English & Weeks, 1987; Rossignol, 1996). The connection of the crural fascia to these muscles may allow for the crural fascia to act as a force transmitter to the limb endpoint during periods of activation. At paw-off, the connection of the posterior biceps femoris and semitendinosus muscles to the crural fascia may facilitate the initiation of swing by effectively increasing the moment arm of these muscles for knee flexion. Having the crural fascia mediate the increase in the acceleration of the joints at the transition point is a more efficient mechanism than using additional muscles to achieve the same goal.

The results of this present study suggest that the crural fascia plays a role in the transmission of force between joints in the hindlimb. The crural fascia connects the posterior biceps and semitendinosus muscles to the calcaneus, thereby effectively making them triarticular muscles. Previously it had been proposed that the proximal muscles are the major force producing muscles while the distal musculature remains more compliant in order to provide an appropriate mechanical interface with the ground during locomotion (Daley, Felix, & Biewener, 2007). The results presented in this article suggest that the crural fascia acts as the proximodistal force transmitter reducing the need for additional or larger muscles in the distal limb. This has been previously suggested by van Ingen Schenau (1994) where it was noted that strong tendons couple the hamstrings to the calcaneus in the cheetah and that this connection allows for the combination of hip extension, knee flexion, and plantar flexion required for strong propulsive movements. Given the anatomical similarity of the crural fascia bands to the cheetah tendons and the loss of acceleration at all three joints post fasciotomy, we suggest that bands may have a similar role in the hindlimb of the domestic cat.

One limitation of the experimental design was the fixation of the tail as the rigid clamp and the subsequent reduced load bearing on the hindlimbs. The reduced load-bearing with consequent reduction in activity of antigravity muscles along with the imposed stabilization of the clamp is likely to have led to an underestimate of the potential effects of the fasciotomy.

Variability—The finding of increased variability of the limb segments and limb endpoint after complete fasciotomy suggests that the disruption of the crural fascia might have changed the tension balancing forces within the limb. The change in tension could have occurred in a force dependent manner, which could be explained by the activation of multiple muscle groups in the limb. As the hamstrings contract more strongly during locomotion, there will be an increase in tension in the crural fascia (Carrasco & English, 1999; Hyde et al., 1999), which may in turn restrict the movement in the medial-lateral direction leaving the distal musculature to regulate stiffness in the distal limb mainly in the sagittal plane. The hamstring muscles insert medially or laterally onto the tibia contributing to internal and external rotation of the shank. Simultaneous activation of these muscles would tend to stabilize the shank about this axis, but the transmission of some of the force diagonally through the cross fibers (Stecco et al., 2009) observed in the sheet of the crural fascia to the opposite side could reinforce the stabilizing effect. This mechanism may reinforce the stabilization of the ankle by cocontraction of the ankle stabilizer muscles and the reciprocal inhibition between them (Bonasera & Nichols, 1996). Furthermore, the gastrocnemius muscles have been shown to be strong abductors and plantarflexors (Lawrence, Nichols, & English, 1993). In particular, the medial gastrocnemius muscle is known to produce a strong abduction force due to its lateral insertion into the calcaneal tendon. This could be balanced during locomotion by contraction of the hamstrings muscles due to the medial insertion of the crural fascia bands onto the calcaneus. However, during standing or when the hamstrings are not strongly activated, the medial gastrocnemius muscle may produce a larger abduction torque, and contribute to the laterally directed forces in response to horizontal perturbations (Macpherson, 1988).

Donelan and Pearson (2004) noted that higher order nervous system centers have been suggested to play a large role in the control of the limb in the frontal plane. Our results suggest that after fasciotomy the tensile structure of the crural fascia has been disrupted and is no longer able to transmit or maintain the tension and in turn may be a reduction in the local control of the degrees of freedom. Although this reduction in tension and corresponding increase in variance does not indicate that the system is unstable, the increased variance of the trajectory of the limb may lead to instability, as suggested by the loss of medialateral control demonstrated by reducing weight support (see Results section).

The increase in variance was smaller in the sagittal plane kinematics due to the constraints of the experiment, head and tail fixation and walking on a treadmill belt, as well as passive stability that is maintained in the plane of progression (Bauby & Kuo, 2000). The passive stabilizing effect would not have been as great in the medialateral direction since the action is perpendicular to the forward movement of the animal, so removal of the crural fascia would not be as completely compensated by the dynamics of the limb, potentially resulting in the increased variability observed. The sagittal plane effects would presumably be greater in animals running over ground, where body fixation is absent. The mechanical coupling between frontal and sagittal plane mechanics implies that increases in frontal plane variability would influence sagittal plane mechanics under these conditions.

Tensegrity

The effects of fasciotomy on acceleration at the ankle and knee joints support the first hypothesis and appear to arise from the specific connections between the distal hamstrings muscles and the calcaneus. The influence of fasciotomy on kinematic variability and presumably stability speaks to a more general function of the crural fascia, and that is to support a three-dimensional network of connective tissue, with embedded muscles and with bony attachments, that forms a tensegrity structure during activity. The conformation of this network would of course vary as the patterns of muscular activity vary during the evolution of the movement, resulting in the desired kinematics for a given set of environmental loading conditions. This presumed network would help to unify the parts of the limb and contribute to the regulation of task-level variables, such as limb orientation and limb length (Chang, Auyang, Scholz, & Nichols, 2009). The results reported here demonstrated that disruption of this network has ramifications for limb control beyond the limb segment in which the disrupted fascia is located or joints crossed by the fascia. Kinematic changes were noted at the knee and hip, and increased variance of limb orientation occurred in the frontal plane. These observations indicate that control of limb movement is accomplished in a holistic fashion rather than in a modular way by the independent control of the joints. Any perturbation of the network is communicated throughout the network and the mechanical response is fully integrated. This arrangement contributes substantially to the reduction in degrees of freedom of the system, in a task-dependent manner, and therefore assumes some of the computational burden of motor control.

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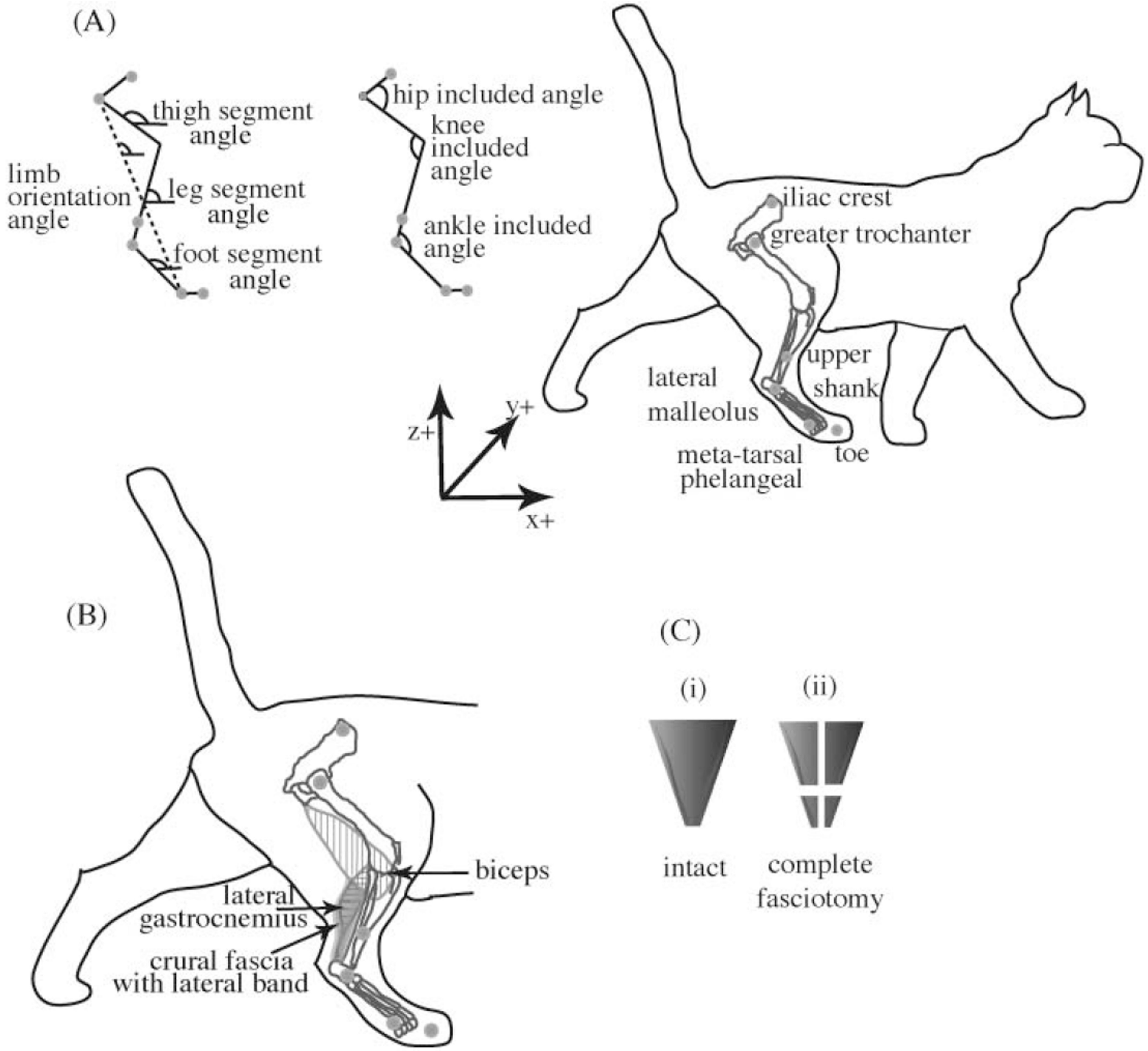

FIGURE 1.

(A) A stick figure representation of the right feline hindlimb showing the segment and joint angles as well as the coordinate system used. The stick figures align with the anatomical markers placed on the cat. (B) The location of the crural fascia on the posterior distal limb. (C) The two fascia states, in sequential order of disruption, as viewing the crural fascia from behind the right hindlimb. The first depicts the crural fascia sheet intact and the second after a complete fasciotomy involving splitting the sheet longitudinally and then cutting through the medial and lateral bands.

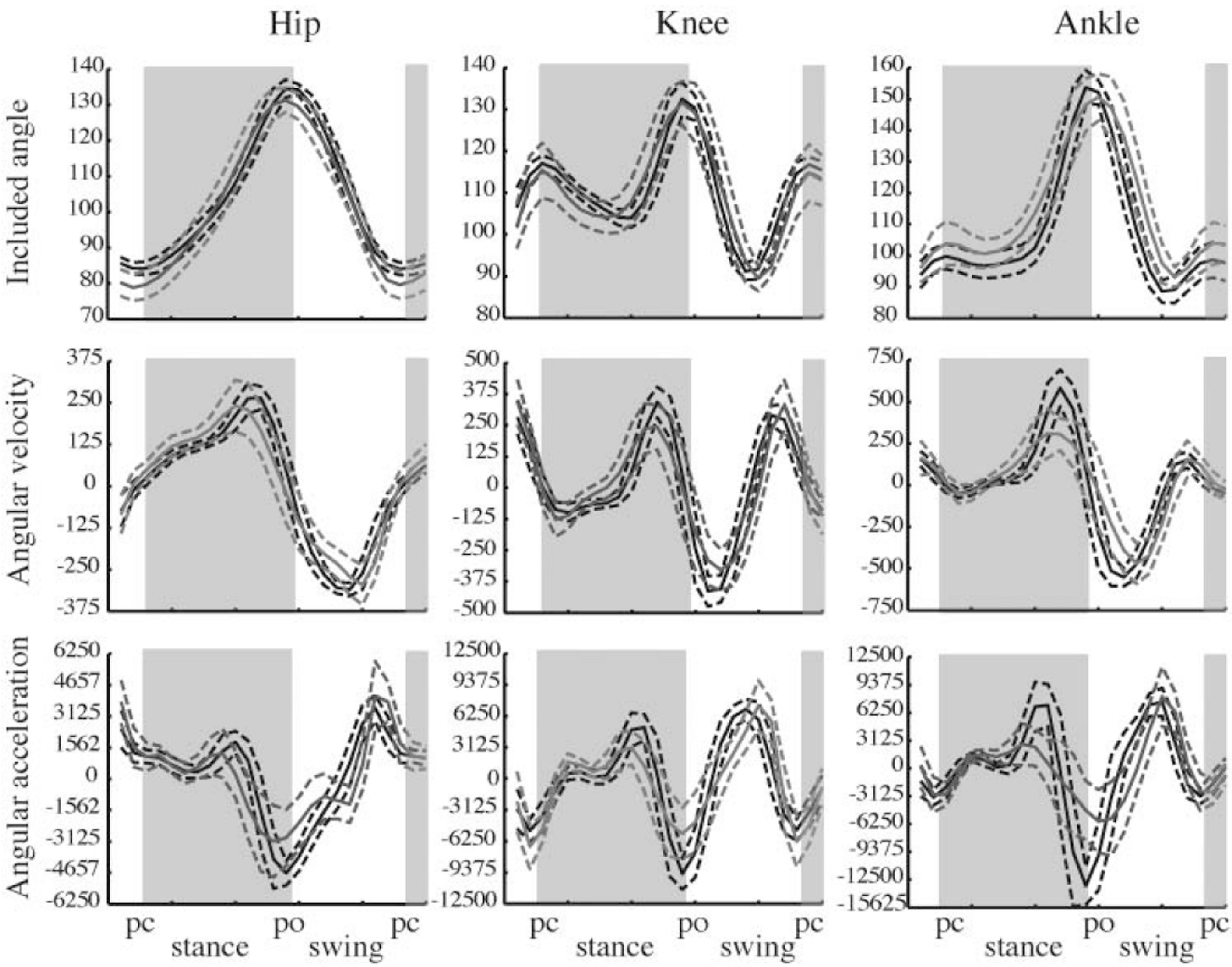

FIGURE 2.

The joint angles of the hip, knee, and ankle are plotted horizontally with the corresponding angular velocities and accelerations plotted vertically. The black lines represent the intact case and the grey lines the complete fasciotomy. The dashed lines represent the standard deviations. This figure shows a representative cat. The gray background represents stance (from paw contact [pc] to paw-off [po]) and the white background represents swing. While in this animal there is no significant change in the joint angles, there is a significant change in the angular accelerations, particularly at paw-off.

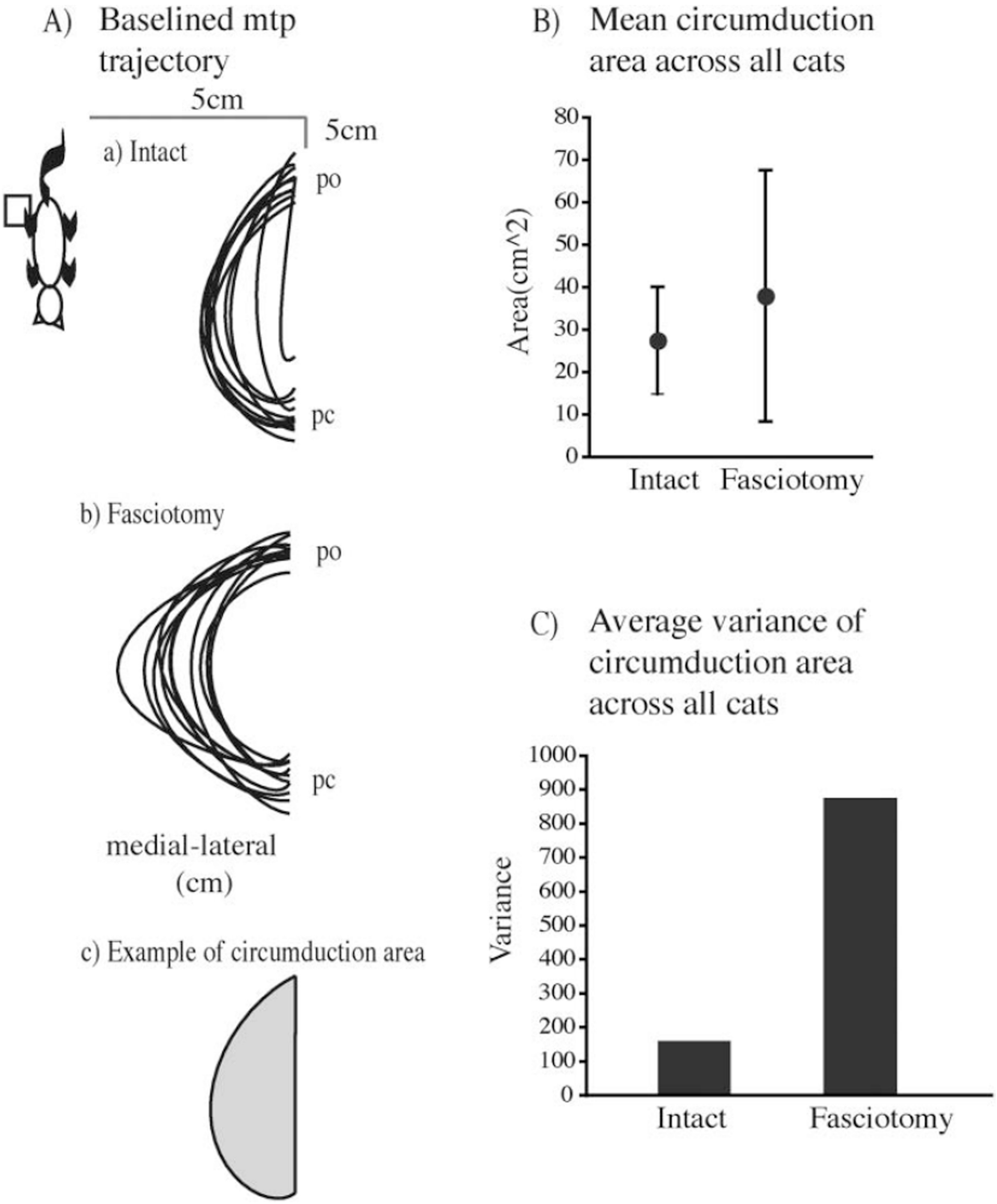

FIGURE 3.

(A) Depicts the swing trajectory of the MTP marker for one representative cat with the fascia (a) intact and (b) complete fasciotomy, as well as (c) a representative area for a step. Note the increased excursion and variance. (B) The mean excursion area for six cats with intact and complete fasciotomy conditions. There is an increase in the circumduction area. (C) The marked increase in average variance across all six cats.

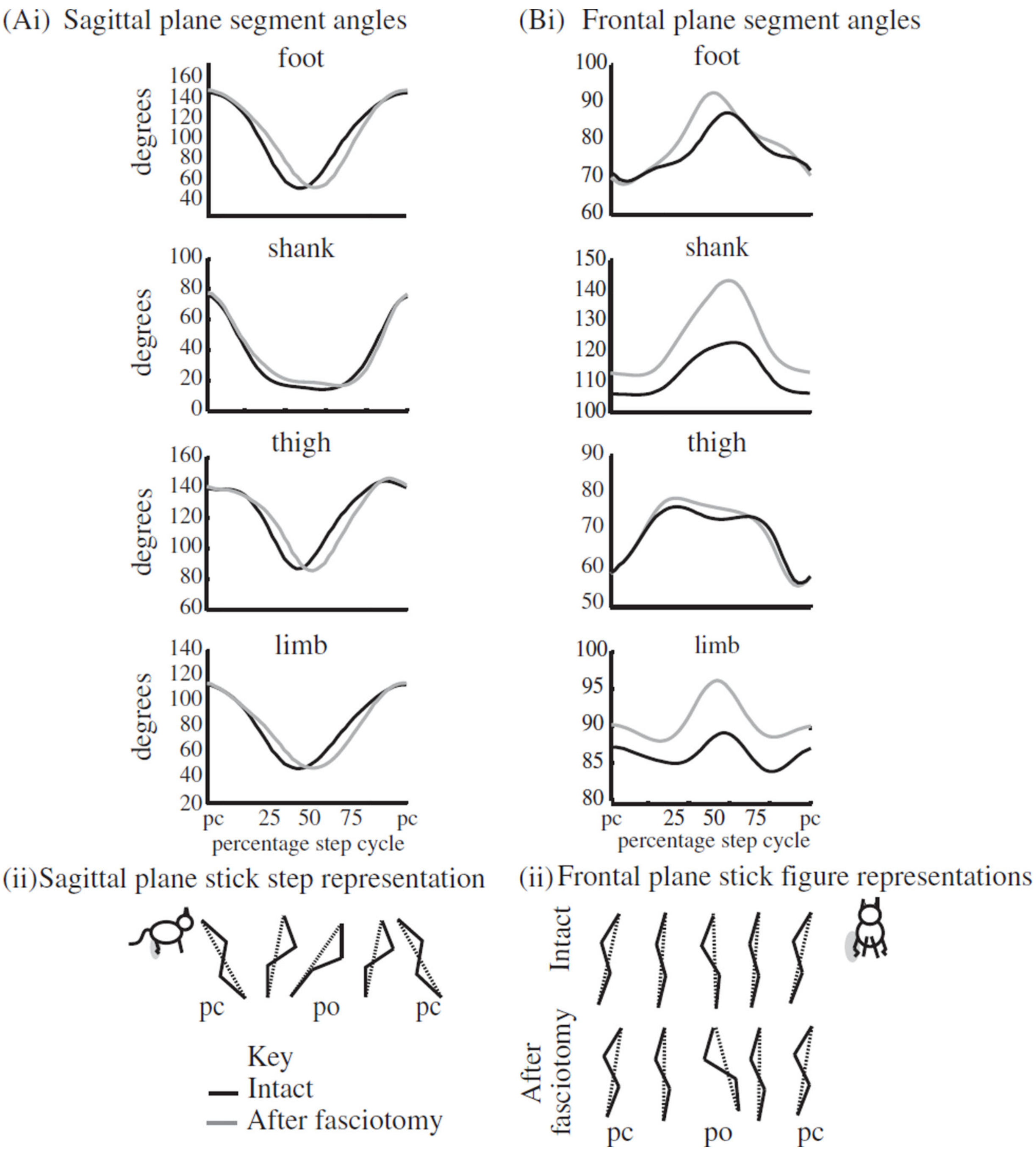

FIGURE 4.

The (A) sagittal plane segment does not show a significant change in trajectory upon the disruption of the crural fascia in the representative cat. (B) The frontal plane shows a shift in trajectory of the limb orientation, which can be attributed to the changes in the shank and foot segment angles upon complete fasciotomy. (ii) Stick figure representations showing the orientation of the limb through the step cycle.

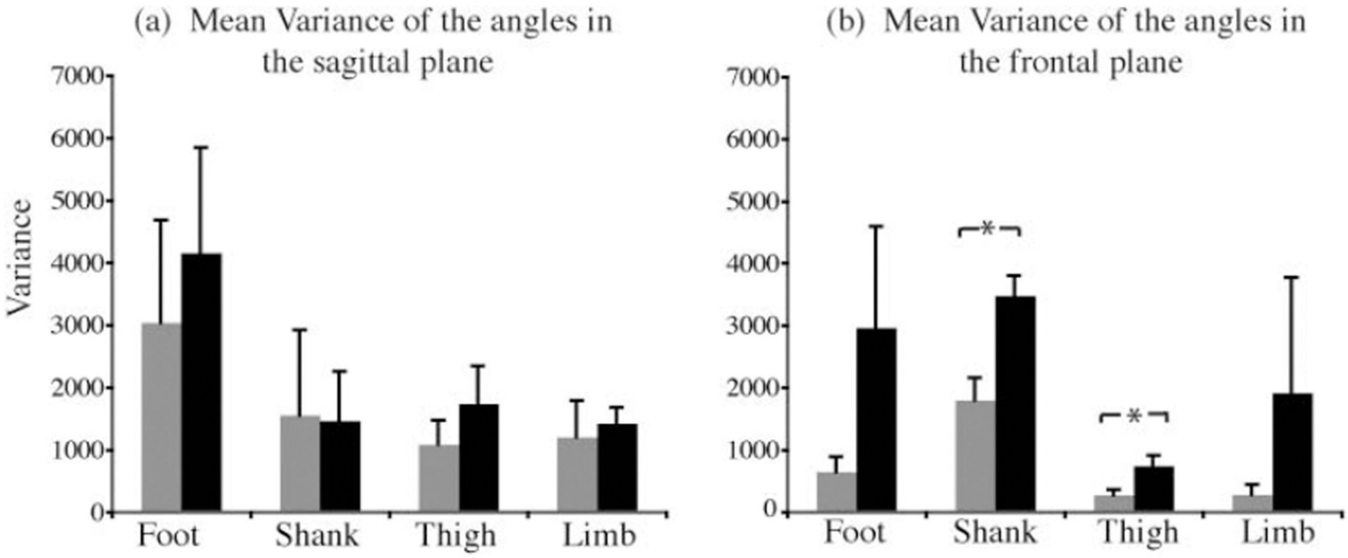

FIGURE 5.

The mean variance across all cats for the foot, shank, thigh, and limb segments in the (A) sagittal and (B) frontal planes. The shank and thigh segment in the frontal plane show a statistically significant increase in variance upon fasciotomy. The grey bars represent intact crural fascia case and the black bars represent the complete fasciotomy case.

TABLE 1

Mean Data Across All Trials for an Example Cat at Paw Contact, Max Acceleration At Each Joint, Paw Off and Mid Swing During the Step Cycle

Variable	**Pre**	**Post**	**# Matched**	**# Stat and *p***
Paw contact				
Hip angle	98.9	95.6	3 decreased	3, < .004
Hip velocity	−75.2	−85.1	4 increased	1, < .0001
Hip acceleration	3056.8	3845.1	3 decreased	3, < .0001
Knee angle	113.3	109.8	3 decreased	2, < .043
Knee velocity	182.4	255.1	5 increased	1, < .0001
Knee acceleration	−5411.6	−6598.4	3 decreased	3, < .0001
Ankle angle	97.8	100.1	3 decreased	1, < .0001
Ankle velocity	103.4	145.8	4 decreased	2, < .04
Ankle acceleration	−3428.3	−2663.9	4 decreased	4, < .04
Max acceleration during stance				
Hip angle	98.6	95.2	5 decreased	5, < .03
Hip velocity	−68.5	−73.3	4 increased	2, < .03
Hip acceleration	3072	3884	2 decreased	2, < .0001
Knee angle	105.2	106.2	3 increased	2, < .028
Knee velocity	176.1	134.2	2 increased	2, < .003
Knee acceleration	6526	4203	4 decreased	4, < .035
Ankle angle	106.8	102.4	3 increased	2, < .009
Ankle velocity	369.8	224.2	3 decreased	3, < .0004
Ankle acceleration	9522	3927	4 decreased	4, < .006
Paw-off				
Hip angle	144.9	141.6	4 decreased	4, < .025
Hip velocity	10.7	−65.9	4 decreased	2, < .025
Hip acceleration	−2294	−1618	3 increased	1, < .0001
Knee angle	134.5	132.5	3 increased	1, < .02
Knee velocity	−66.6	−190.3	4 increased	2, < .0008
Knee acceleration	−1055.9	622	3 decreased	1, < .035
Ankle angle	157.5	155.8	3 increased	1, < .008
Ankle velocity	−57.4	−30.7	4 increased	1, < .013
Ankle acceleration	−1451.4	911.6	3 decreased	2, < .0001
Midswing				
Hip angle	122.2	112.8	5 decreased	3, < .002
Hip velocity	−288.8	−280.8	3 decreased	2, < .001
Hip acceleration	165.7	306.3	3 increased	1, < .008
Knee angle	116.6	115.9	4 decreased	1, < .008
Knee velocity	−463.9	−384.9	3 decreased	3, < .006
Knee acceleration	634.3	488.1	4 decreased	1, < .001
Ankle angle	132.8	126.7	4 decreased	4, < .008

Variable	**Pre**	**Post**	**# Matched**	**# Stat and *p***
Ankle velocity	−600.1	−519.1	4 decreased	4, < .021
Ankle acceleration	697.9	643.4	3 decreased	1, < .0075

Note. The number of cats that showed the main trend are listed as well as the number of those cats that showed a significant change in direction with the *p* values.