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INTERACTION BETWEEN TENDON COMPLIANCE AND ACTIVATION LEVEL ON FIBER OPERATING LENGTHS OF SKELETAL MUSCLE

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SUMMARY

This study explored the sensitivity of skeletal muscle isometric operating lengths to activation level. Using a musculoskeletal model of the guinea fowl hind limb we found that low-compliance muscle-tendon units (parallel fibered hip muscles) have operating lengths that are insensitive to activation level. High-compliance muscles (distal leg muscles with prominent external tendons) on the other hand operate on different regions of their force-length curve depending on activation level. The interaction between activation, tendon compliance and muscle fiber operating lengths may impact muscle recruitment strategies.

INTRODUCTION

The region over which skeletal muscles operate on their force-length (F-L) relationship is fundamental to the mechanics of movement. Function at the plateau region of the F-L curve (near the muscle's optimal length; L_0) may be regarded as favorable since force capacity is optimized.

The activation level of a muscle at a given posture will, to a large extent, dictate its force output and will therefore affect tendon stretch and subsequently muscle fiber lengths. Similar to Arnold and Delp [1], we used modeling and simulation to test whether muscle-tendon units with high tendon compliance have a restricted range of activation levels over which optimal fiber lengths can be achieved compared to muscles with low tendon compliance. Furthermore, we hypothesized that among those muscles with high tendon compliance, some may achieve optimal fiber lengths under low forces (low activation) whereas others may achieve optimal lengths under high forces for a given joint posture. This interaction between activation and muscle and tendon lengths may have an important influence on muscle recruitment strategies.

METHODS

To assess the effect of activation and tendon compliance on muscle fiber operating lengths we developed a musculoskeletal model of the guinea fowl (*Numida meleagris*) hind limb (OpenSim; [2].) capable of simulating muscle activation, force, and length under various conditions. The guinea fowl was selected as a model animal of choice because 1) it possesses a wide scope of muscle-tendon architectures ranging from muscle-tendon units with very low tendon compliance (typically hip muscles) to those with very high tendon compliance (typically ankle and toe muscles) and 2) because it was possible to obtain accurate experimental measurements of muscle-tendon architecture and material properties.

An 18-degree-of-freedom model of the pelvis and lower limb was constructed with 57 muscle lines of action (Fig.1). Muscles with broad origins and insertions were divided into 2 or more separate muscle lines. Muscle/tendon paths were digitized using a custom built 3D surgical digitizing arm (KneeNav; Stanford, CA). Joint coordinate systems were defined from functional joint centers and axes of rotation determined from 3D motion capture of the joints' range of motion using a Vicon 10-camera motion capture suite (Oxford Metrics, Oxford, UK). Muscle and tendon masses were measured from fresh/frozen specimens. Fiber lengths and pennation angles were measured from formalin-fixed specimens and used to calculate muscle physiological cross sectional area. Optimal fiber lengths (L_0) were calculated by scaling measured fiber lengths by the ratio of the measured sarcomere lengths to optimal sarcomere lengths. Sarcomere lengths were measured using second-harmonic generation laser scanning microscopy [3] and optimal sarcomere length was calculated from known filament lengths [4]. Individual tendon stress/strain curves were determined using a material testing rig equipped with freeze clamps (Bosch, Broadview, IL). Tendon slack lengths were determined as the tendon length that resulted in a match between predicted and measured fiber lengths at a specified joint posture.

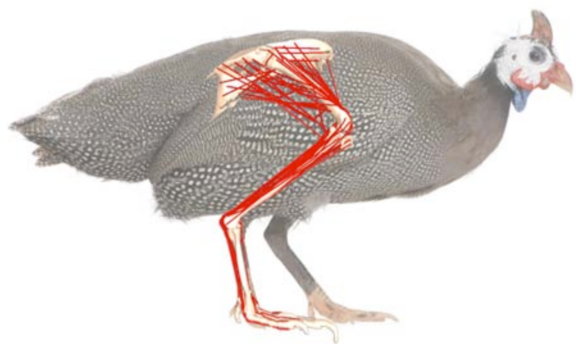

Figure 1: Guinea fowl with superimposed musculoskeletal model.

A Muscle was categorized as low compliance if its ratio of tendon / muscle fiber length was < 2 and high compliance if the ratio was > 2. This categorization resulted in nearly all proximal (hip and knee) muscles grouped as low compliance and all distal (ankle and toe) muscles as high compliance. Normalized muscle fiber operating lengths were therefore simulated for proximal muscles under isometric contractions across the hip range of motion (other joints set to angles corresponding to passive joint torques) at activations ranging from 0.5% to 100%. The same was done for the distal muscles across the ankle range of motion.

We also assessed the isometric operating lengths of all extensor (antigravity) muscles in a standing posture under low (5%) activation and at the posture corresponding to the mid-stance of fast running for maximal (100%) activation.

RESULTS AND DISCUSSION

The activation level affected the mean isometric operating lengths of the proximal muscles by less than 5% (Fig. 2a). The fibers were longest at low activation (0.74 –1.11 L/L_0) and shortest at the highest activation (0.70 – 1.06 L/L_0). In contrast, the level of activation affected the mean isometric operating lengths of the distal muscles by up to 33%, with the longest and shortest lengths being 0.66 – 1.08 L/L_0 under low activation and 0.57 – 0.81 L/L_0 under maximal activation (Fig. 2b).

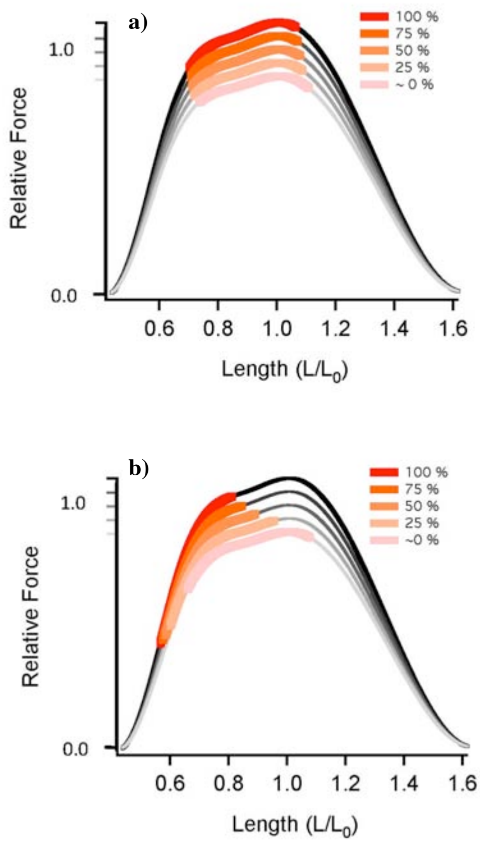

Figure 2: The mean isometric operating lengths from all the proximal (a) and distal (b) muscles across the hip and ankle range of motion, respectively. Increasing activation level is depicted by light to dark colors (see legend).

The isometric operating lengths of the hip and knee extensor muscles were minimally affected by activation level when functional joint postures were simulated (standing posture for low activation, running posture for high activation). However, the isometric operating lengths of the distal muscles were strongly affected by activation level in these postures. Interestingly, the mean operating lengths of the gastrocnemius muscles were closer to L_0 at low activation during standing compared to the mean operating lengths of the digital flexor muscles, which operated closer to L_0 under high activation in a running posture (Fig. 3.).

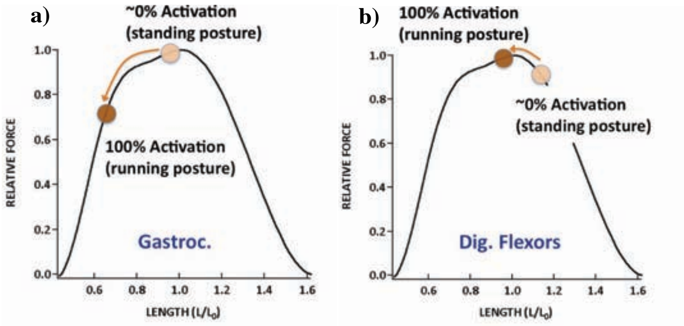

Figure 3: The mean isometric operating lengths of the gastrocnemius muscles (a) and digital flexor muscles (b) during simulated low activation (standing posture) and high activation (mid stance of fast running).

CONCLUSIONS

Activation-dependent tendon stretch can have a marked effect on where muscles operate on their force-length curve. We found this affect is present in muscle-tendon units with high compliance (in particular distal leg muscles) but not in low-compliance muscle-tendon units (the majority of proximal leg muscles). Under certain joint postures the effect of tendon stretch may significantly limit the ability to produce high forces in the distal leg muscles (Fig 2b).

Interestingly, in certain muscle-tendon units, such as the gastrocnemius muscles, the operating lengths are near optimal under low activation conditions (low tendon stretch). In contrast, the synergist digital flexor muscles achieve optimal lengths at high activation (high tendon stretch). This difference may influence muscle recruitment patterns. For example, preferential recruitment of the gastrocnemius and digital flexor muscles for low and high force requirements, respectively, would result in a reduction in overall muscle activation.

Future studies aim to address the interaction between tendon compliance, activation and muscle operating lengths under dynamic conditions.

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