

FUNCTIONAL HETEROGENEITY WITHIN AND BETWEEN HIND LIMB MUSCLES DURING RUNNING IN GUINEA FOWL

Timothy E. Higham and Andrew A. Biewener

Harvard University, Bedford, MA, USA
E-mail: thigham@fas.harvard.edu

INTRODUCTION

Terrestrial vertebrates employ limb muscles to control movements of the skeletal system or to counterbalance loads (Biewener and Gillis, 1999). The complex activation patterns within muscles have long been identified using electromyography (e.g. English, 1984) and, in recent years, some of the complex patterns of *in vivo* muscle length changes have been elucidated using techniques such as Magnetic Resonance Imaging (Pappas et al., 2002), geometric modeling (Gregor et al., 2006), and sonomicrometry (Soman et al., 2005).

Muscles are often heterogeneous, exhibiting spatial variation in recruitment, fiber type composition, and force generation. Unequal shortening within a muscle can be due to several factors including, for example, muscle architecture (Pappas et al., 2002) and fiber type regionalization (Chanaud and Macpherson, 1991). Understanding how this heterogeneity in muscle shortening translates into overall muscle function is imperative for understanding how the musculoskeletal system can adapt to changes in demand placed upon the locomotor system.

Muscle synergists, such as the lateral (LG) and medial (MG) gastrocnemius muscles of terrestrial vertebrates, can also vary considerably in fiber type composition, architecture and recruitment patterns. Having multiple muscles acting at the same joint provides flexibility with regards to optimal function. For example, one of the

muscles might be optimized for ballistic movements while another might be optimized for slow, steady movements. Understanding the differences in function between synergists will provide insight into the role of redundancy in the musculoskeletal system.

The goals of this study are to address the following two questions using guinea fowl: 1) Do the proximal and distal regions of the MG exhibit similar fascicle strain and activation patterns? 2) Do the MG and LG exhibit similar fascicle strain, activation and force patterns?

METHODS

Adult guinea fowl (*Numida meleagris*) were used in this study, and data were collected from four individuals. Each individual was trained to run on a motorized treadmill. Muscle activation patterns were quantified by inserting fine-wire bipolar EMG hook electrodes into the proximal and distal regions of the LG and MG. Muscle length patterns were quantified by inserting 2mm sonomicrometry crystal pairs into the two muscles. One pair was implanted into the LG and two pairs (proximal and distal locations) were implanted into the MG. The two crystals of a pair were separated by approximately 1cm. Forces exerted on the tendons of each muscle were measured using E-type stainless steel tendon buckle force transducers. One high-speed Photron camera (250 frames per second) was used to capture hind limb movements of the guinea fowl during the experiment.

In order to alter the demand placed upon the locomotor system, each bird ran on a level and uphill surface, and at speeds ranging from 0.5 m/s to 2.5 m/s. Following each experiment, the bird was euthanized and the location of the electrodes and crystals were verified. Several morphological measurements were recorded for the muscles and tendons.

RESULTS AND DISCUSSION

Activation of the LG and MG preceded the onset of force, which occurred at the beginning of the stance phase of the stride. The onset of force generation in the LG was

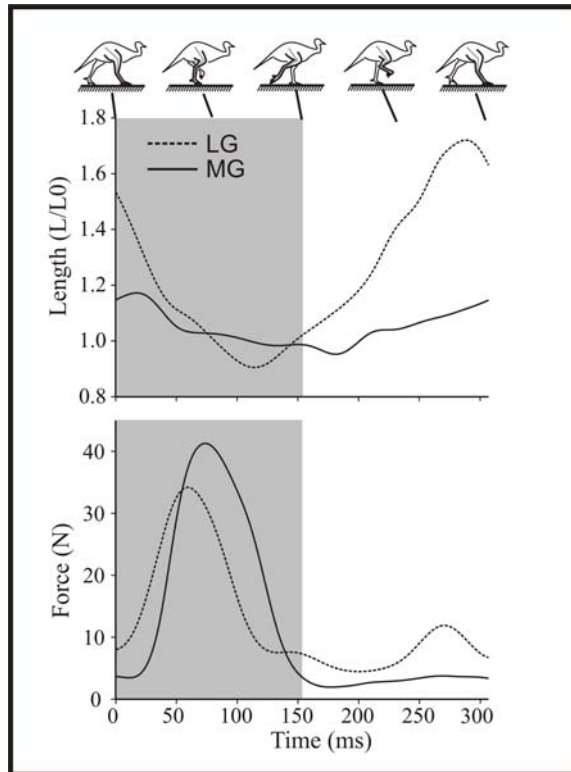


Figure 1: Relative length (upper panel) and force (lower panel) from the lateral (LG) and medial (MG) gastrocnemius muscles for a guinea fowl running on a level treadmill at a speed of 2 m/s. Note that the shaded area indicates the stance phase of the stride.

coincident with footfall, whereas the MG began generating force after the LG by an average of 6.6 ± 0.8 ms (Fig. 1). The MG and LG differed in the amount of force generated relative to the amplitude of their fascicle strain patterns, indicating that work output differed between these muscles.

Fascicle strain was greater in the proximal MG compared to the distal MG at all speeds and inclines. For example, when running on a level surface at a speed of 2 m/s, the proximal and distal MG shortened at the beginning of stance by $17 \pm 0.4\%$ and $1 \pm 0.1\%$, respectively. This suggests that the proximal portion of the MG is doing more work and contributing more to power production at the ankle than the distal portion of the MG. The decrease in strain along a proximal-distal axis appears to be a common theme within muscles as well as within limbs of terrestrial vertebrates.

REFERENCES

- Biewener, A.A., Gillis, G.B. (1999). *J. Exp. Biol.*, **202**, 3387-3396.
- Chanaud, C.M., Macpherson, J. M. (1991). *Exp. Brain Res.*, **85**, 271-280.
- English, A.W. (1984). *J. Neurophysiol.*, **52**, 114-125.
- Gregor, R. J. et al. (2006). *J. Neurophysiol.*, **95**, 1397-1409.
- Pappas, G. P. et al. (2002). *J. Appl. Physiol.*, **92**, 2381-2389
- Soman, A. et al. (2005). *J. Exp. Biol.*, **208**, 771-786.

ACKNOWLEDGEMENTS

This research was supported by NIH Grant AR047679. We thank Pedro Ramirez for animal care.