ISOMETRIC FORCE PRODUCTION REQUIRES ASYMMETRIC MUSCLE-TENDON LENGTH TRAJECTORY

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INTRODUCTION

During cyclic movements (e.g. running, walking) muscle fibers at distal joints produce force nearly isometrically and perform very little mechanical work. Elastic tendons in series with the muscle fibers store and return elastic energy in the interaction with the external environment to maintain steady speed [1, 2]. The goal of this study was to determine the muscle-tendon (MT) length trajectory required to maintain isometric, strut-like behavior of the muscle fibers in series with a highly compliant free tendon. We hypothesized that the MT length change pattern during a feedback controlled supramaximal isometric contraction would be asymmetric, reflecting the rapid rise and slower relaxation that is characteristic of muscle force production. Furthermore, we expected that peak muscle-tendon lengthening velocity during isometric contraction would exceed the peak muscle fiber shortening velocity observed during a 'fixed-end' (i.e. MT velocity = 0) contraction of the same duration.

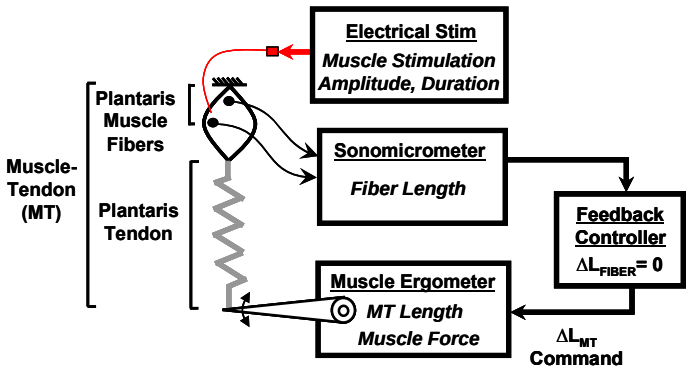

Figure 1. Schematic of the experimental apparatus. When the muscle was stimulated via the sciatic nerve (red arrow), a proportional integral derivative (PID) controller used sonomicrometer length feedback to generate a control signal for ergometer position. The PID control algorithm commanded the ergometer to adjust muscle-tendon (MT) length in order to keep muscle fibers isometric throughout the contraction. For example, upon stimulation, initial fiber shortening would be prevented by a feedback control signal to the ergometer to apply a rapid MT lengthening response.

METHODS

We isolated a bullfrog (*Rana catesbeiana*) plantaris muscle-tendon unit (plantaris muscle mass = 2.8 g, MT length = 64 mm; free tendon length = 30 mm) and surgically implanted a pair of sonomicrometry crystals (1 mm diameter) along the line of action of the plantaris muscle fibers. We attached a nerve-cuff to the sciatic nerve and the muscle-tendon to an ergometer under position control. Using a 4V, 50 ms pulse train (0.2 ms pulses, 100 pps), we supramaximally stimulated the muscle during two conditions. First, by keeping the ergometer position (and MT length) fixed we determined how much and how fast maximally stimulated plantaris muscle fibers would shorten against the series elastic plantaris tendon (i.e. 'fixed-end' contraction). Next, we used real-time feedback of plantaris fiber length from the sonomicrometery pair and an optimally tuned feedback controller on the ergometer to drive the MT through a length change pattern that prevented the plantaris fibers from shortening (i.e. we enforced isometric force production) (**Fig. 1**). For both conditions we set the rest length of the MT to correspond with the onset of passive force from an experimentally determined force-length curve (~1 N initial tension). We recorded (1) MT force and length from the ergometer and (2) muscle fiber length from the pair of surgically implanted sonomicrometry crystals.

RESULTS

In order to maintain muscle fibers isometric (**Fig 2., blue**), the ergometer applied a highly asymmetric MT length trajectory (**Fig 3., middle, blue**). The MT lengthened rapidly early in the contraction and then slowly shortened late in the contraction, mirroring the pattern of force development of the muscle fibers (**Fig 3., top, blue**). In contrast, during the 'fixed-end' contraction, muscle fibers shortened

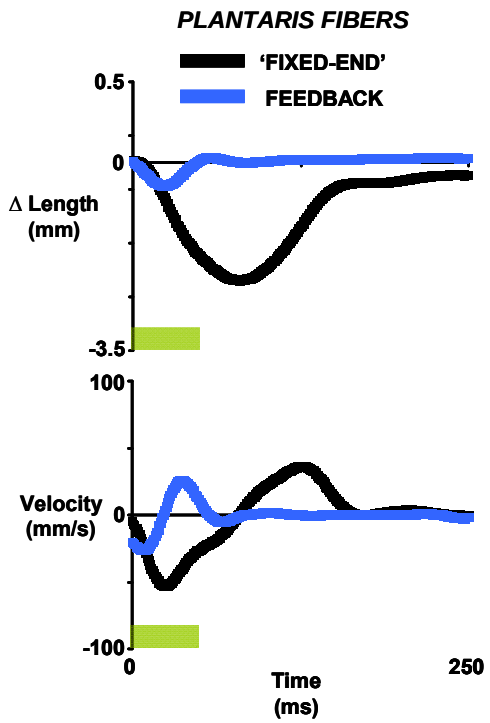

Figure 2. Length change (mm), and velocity (mm/s) versus time (ms) records from sonomicrometer crystal pair impanted in line with the plantaris muscle fibers during a 'fixed-end' (black) and feedback controlled (blue) contraction. The shaded green bars represent the period of supramaximal stimulation (50 ms). In the feedback condition, the muscle fibers remain nearly isometric. In the 'fixed-end' condition, the muscle-fibers shorten considerably against the series tendon.

considerably against the series elastic plantaris tendon (**Fig.2, top, black)**. The peak MT lengthening velocity (+153 mm/s) required to maintain fibers isometric was nearly three times as fast as the peak muscle fiber shortening velocity (-52 mm/s) during the 'fixed-end' contraction and considerably higher than the maximum shortening velocity for plantaris fibers (~ -70 to -100 mm/s). MT peak force was markedly higher (+87%) in the feedback controlled isometric contraction when compared to the 'fixed-end' contraction (**Fig. 3, top**).

CONCLUSIONS

These results suggest that an asymmetric muscle-tendon length change pattern may be required for isometric force production in a compliant muscle-tendon. The results also highlight a potentially important trade-off. Because of the rapid MT lengthening that is required to maintain fibers isometric, it may be difficult to avoid muscle fiber shortening against the series tendon and costly muscle fiber positive work in a highly compliant muscle-tendon. On the other hand, a MT that is too stiff may limit the possibility for economical isometric force production and elastic energy storage and return. Further studies might explore the effects of varying series stiffness on the requirements for isometric force production in a muscle-tendon unit.

REFERENCES

(1) Roberts, T.J. et al. (1997). *Science*, 275(5303):1113-1115.

(2) Ishikawa, M. et al. (2005). *J Appl Physiol*, 99(2):603-608.

ACKNOWLEDGEMENTS

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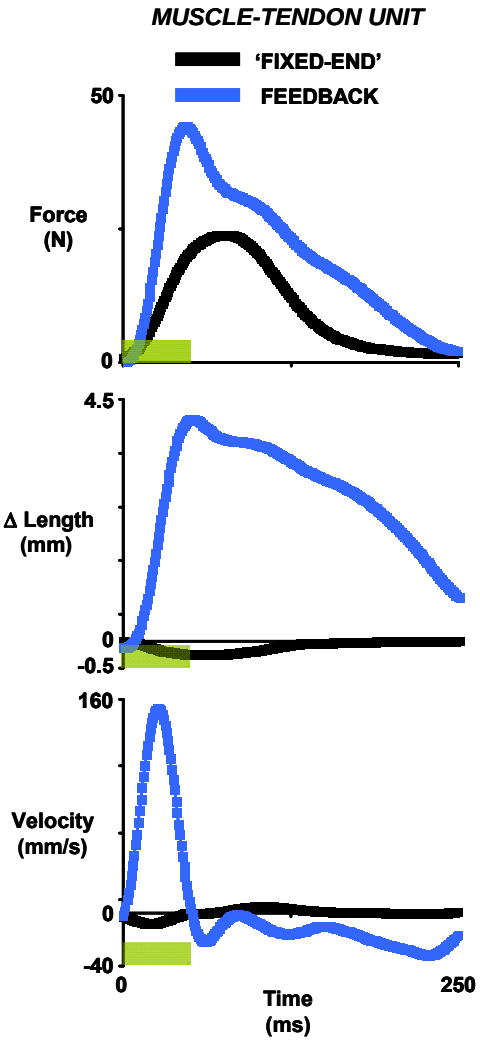

Figure 3. Force (N), length change (mm), and velocity (mm/s) versus time (ms) records for the whole muscle-tendon unit during a 'fixed-end' (black) and feedback controlled (blue) contraction. The shaded green bars represent the period of supramaximal stimulation (50 ms). In the feedback condition, the muscle-tendon is rapidly lengthened by the ergometer to keep muscle fibers isometric. In the 'fixed-end' condition, the muscle-tendon does not change length and the muscle fibers shorten against the series tendon.