

Modeling muscle-tendon dynamics during walking in aged rats (*Rattus norvegicus*)

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INTRODUCTION

Locomotion is more energetically costly in older individuals. The use of elastic energy storage and recovery in tendons has been thought to reduce the metabolic cost of locomotion (Cavagna et al. 1964). However this may be compromised in the elderly when both the active and passive muscle-tendon properties change.

Here we report the results of model simulations on the cyclical behavior of muscle-tendon units. The model consists of a Hill-type muscle model in series with a linearly elastic tendon. All model parameters were measured experimentally in young and aged rats.

MATERIALS AND METHODS

Active and passive muscle-tendon unit properties of the medial gastrocnemius (MG) and its distal tendon were measured *in situ* in young (n=8, age 5-9 months, body mass 362±32 g) and old (n=8, age 33-34 months, body mass 489±19 g) male Brown Norway x F344 F₁ hybrid rats, *Rattus norvegicus*, from the National Institutes of Aging (F344BN; National Institute on Aging, Bethesda, MD).

We used a Simulink (MathWorks®, Natick, MA) computational model ¹, with the empirically measured parameters taken from old and young rats as model inputs. Young and old muscle-tendon units were oscillated at 3Hz through stretch-shorten cycles starting at $1.1L_{0 \text{ muscle}}$ with amplitudes equal to 25% of the MTU resting length. The muscle was stimulated with a 10% duty cycle at 37.5% of stretch-shorten cycle (this was found to reduce active muscle work).

For old MTUs we tested an additional condition: cycles started at $1.0L_{0 \text{ muscle}}$ and had reduced amplitudes of 12% MTU resting length to

match the passive force developed before stimulation in the young MTU. The high passive stiffness of both the muscle and tendon in old rats requires high forces to be applied to the MTU either from an antagonist muscle or an increased inertial-gravitational load, which are not present in the old.

RESULTS AND DISCUSSION

With advanced age there was a reduction in isometric muscle force and an increase in the stiffness of both the muscle and tendon of the medial gastrocnemius in rats.

During simulations, we found that positive muscle work was minimized when the muscles were activated at 37.5% of the cycle from the beginning of lengthening, regardless of MTU age, MTU strain or initial muscle length (Fig. 1). Therefore it is unlikely that differences in the timing of muscle activation or alterations to motor control strategies underlie potential differences in the utilization of elastic energy in elderly individuals. Our first set of simulations compared old and young MTUs moving through sinusoidal length changes starting at $1.1L_0$ and through amplitudes corresponding to 25% MTU strain. While the young contractile element initially shortens internally against the tendon, the old CE produces force nearly isometrically. We also found that a larger proportion of the length change of the MTU is attributed to the stretch of the tendon (SEE) rather than the muscle (CE) in the old MTU. On the other hand, as the MTU is being passively stretched prior to stimulation, the increased stiffness of the muscle and the tendon results in higher passive forces in the old MTU (Fig. 1). This results in higher power inputs to the tendon prior to stimulation in old MTUs.

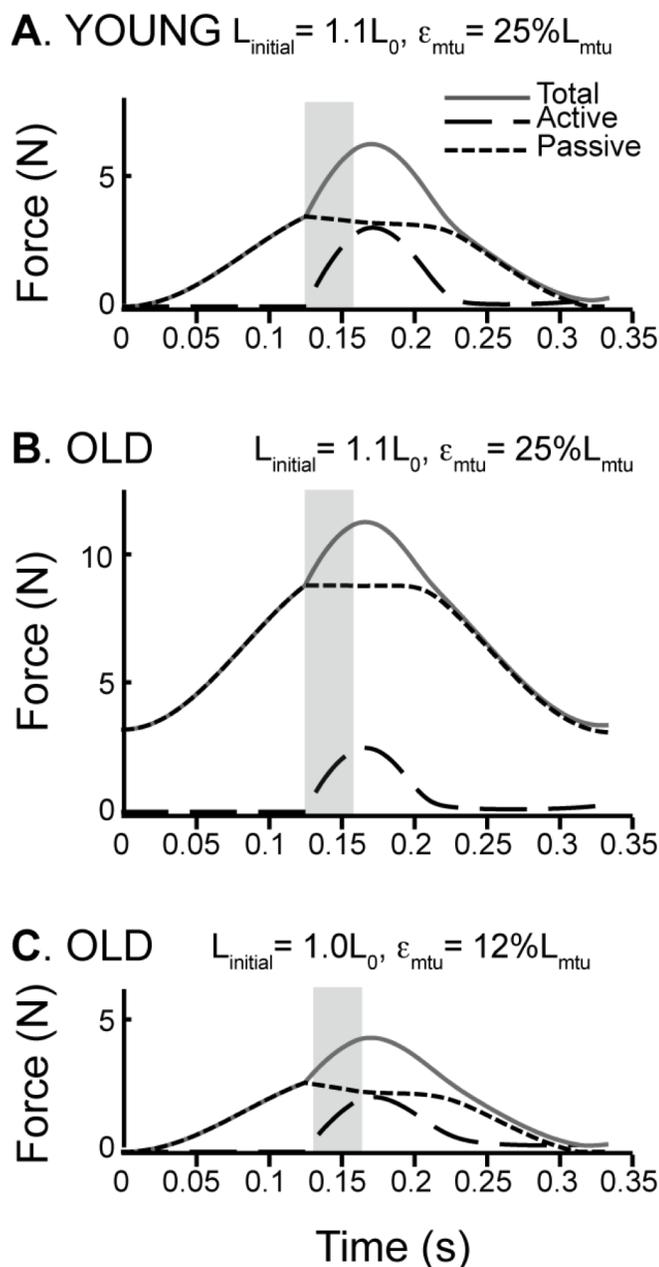


Fig. 1. Time series of force development in the three stimulation conditions tested. When starting length and amplitudes are the same (A and B), the old MTU develops high passive forces prior to activation. When initial passive force and total maximum force are similar (A and C), old MTU develops significantly less power and stores less energy in series elastic elements.

In the reduced initial length and amplitude old simulations we observed a significant decrease in the energy loaded into the tendon prior to

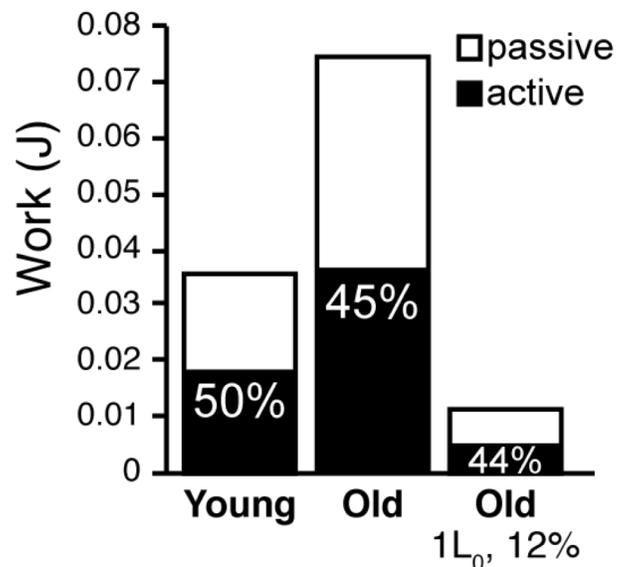


Fig. 2. Active and passive work done during the three simulation conditions. Under realistic conditions, the MG MTU performs less than one third of the total work that a healthy young MTU does.

stimulation onset (Fig. 1C) and a far greater reliance on active forces in the old MTU when compared to simulations at longer lengths. Under these conditions, the MG MTU also performed less total work than a healthy young MTU (Fig. 2).

The reduction in MTU and shorter initial muscle lengths load-matched simulations of old MTUs are physiologically more relevant and potentially explain some of the distinct gait changes that occur with aging in a diversity of animal groups including humans as well as the difference in preferred walking speed and the lower stride length observed in older humans and animals^{3,4} between young and old adults².

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