

# A computational model for the adaptation of muscle and tendon length to average muscle length and minimum tendon strain

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## Abstract

This paper hypothesizes that average muscle length and minimum tendon strain govern muscle and tendon length adaptation in all situations. A model has been implemented to test this hypothesis, and simulations have been performed for normal development, bone lengthening, immobilization, and retinacular release experiments in young and adult animals. The simulation results predict that both muscle and tendon lengthen during normal development, with the rate of tendon growth slowing faster than the rate of muscle growth. The results also predict that muscle length increases during bone lengthening in both young and adult animals, while tendon length increases only in young animals. For immobilization in adult animals, the results predict that muscle length increases when the muscle is immobilized in a lengthened position and decreases when the muscle is immobilized in a shortened position with no change in tendon length. For immobilization in young animals, the results predict reduced muscle growth and increased tendon growth regardless of immobilization position. Finally, the simulations predict that retinacular release which increases excursion of the musculotendinous unit leads to increased muscle length with decreased tendon length in young animals and decreased muscle length with no change in tendon length in adult animals. These simulation results are consistent with experimental findings reported in the literature by other investigators. This suggests that average muscle length and minimum tendon strain may represent general principles that govern muscle and tendon length adaptation.

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## 1. Introduction

Development and maintenance of appropriate muscle and tendon length are essential for normal musculoskeletal function. Insufficient length can contribute to movement abnormalities such as crouch and equinus gait, often necessitating surgical correction (Gage, 1991). Overlengthened muscles and tendons can create even more difficult problems such as calcaneal gait, for which no successful treatment has been established (Segal et al., 1989). To understand how muscles and tendons can be expected to respond to surgical and non-surgical procedures, we must understand how muscle

and tendon length change in response to mechanical stimuli.

Muscles may adapt to their postural length, active functional length, or excursion (Herring et al., 1984), and this adaptation may vary with age or application. Adult muscles increase in length when immobilized in a lengthened position and decrease in length when immobilized in a shortened position (Tabary et al., 1972; Williams and Goldspink, 1978). Muscle length returns to normal with remobilization, and muscles immobilized in one position and moved to a second immobilized position quickly adjust their length to the new position (Tabary et al., 1972). Growing muscles, on the other hand, decrease in length compared with controls for immobilization in both lengthened and shortened positions (Williams and Goldspink, 1971; Williams and Goldspink, 1978). Muscle length increases in young animals following retinacular release which increases muscle excursion while decreasing functional

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length (Crawford, 1954; Koh and Herzog, 1998; Burkholder, 2001).

Fewer studies have addressed tendon adaptation. Tendons lengthen during bone distraction in young dogs (Fink et al., 1999) and shorten following bone shortening in young and adult rats (Tardieu et al., 1983). During immobilization in a lengthened position, tendon length increases rapidly in young rabbits, increases moderately in nearly mature rabbits, and does not change in fully mature rabbits (Tardieu et al., 1977). Immobilization in a shortened position leads to decreased tendon length in immature rabbits (Herbert and Crosbie, 1997).

These experimental findings have led to varying hypotheses for the mechanical regulation of muscle and tendon length, with the proposed stimuli differing with age, application, and investigator (Tabary et al., 1972; Williams and Goldspink, 1973; Gossman et al., 1982; Herring et al., 1984; Herbert and Crosbie, 1997; Burkholder and Lieber, 1998; Koh and Herzog, 1998). This study hypothesizes that the same mechanical stimuli, average muscle length and minimum tendon strain, govern muscle and tendon length adaptation in all situations. A computational model is developed to test this hypothesis in applications including normal development, bone lengthening, immobilization, and retinacular release experiments.

**2. Materials and methods**

The musculotendinous unit (MTU) is idealized as a muscle and tendon connected in series (Fig. 1). Tendon growth occurs throughout the length of the tendon (Crawford, 1950; Fujio et al., 1994; Nishijima et al., 1994) and is therefore described in terms of a specific rate (growth per unit length). Since fibroblasts synthesize the collagen for tendon growth, the maximum specific rate is assumed to depend on cell density which decreases exponentially with age (Ingelmark, 1945).

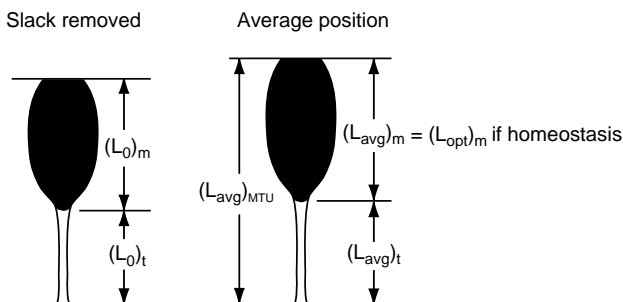


Fig. 1. Schematic of model showing muscle in series with tendon. Tendon slack length  $(L_0)_t$  and muscle zero length  $(L_0)_m$  represent shortest length at which MTU is not slack. Muscle adapts so that muscle optimum length  $(L_{opt})_m$  matches average muscle length  $(L_{avg})_m$  when homeostasis is achieved.

Muscle grows primarily, if not exclusively, at the ends of muscle fibers (Griffin et al., 1971; Williams and Goldspink, 1971). The maximum rate of muscle growth is therefore expressed as a direct rate that is assumed to remain constant throughout life.

Adaptation rules were formulated for tendon slack length  $(L_0)_t$ , representing the shortest length at which the tendon carries load, and muscle optimum length  $(L_{opt})_m$ , representing the length at which the muscle generates maximal active force. Tendon strains are defined as

$$\varepsilon_t = [L_t - (L_0)_t] / (L_0)_t, \tag{1}$$

where  $L_t$  is tendon length during in vivo function. Muscle extension is defined as

$$D_m = L_m - (L_{opt})_m, \tag{2}$$

where  $L_m$  is muscle length during in vivo function.

A tendon grows in length when its minimum strain is positive (tensile). The specific rate of growth is assumed to increase linearly with increasing minimum strain until a maximum rate is reached for strains above 5% (Fig. 2). The 5% strain represents the upper end of normal physiologic tendon strains (Magnusson et al.,

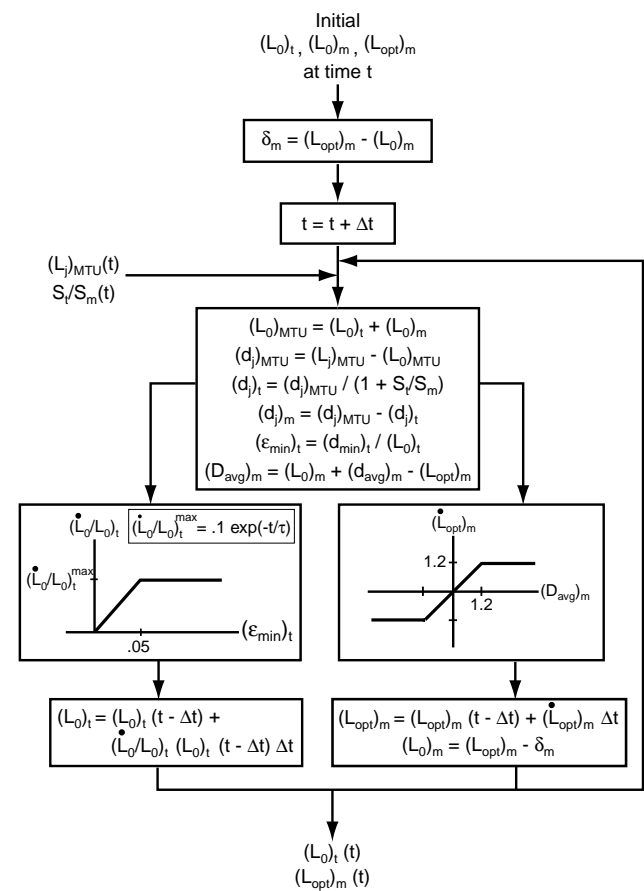


Fig. 2. Algorithm flow chart ( $j = \text{min, max, avg}$ ).

2001; Muramatsu et al., 2001). The maximum specific rate of tendon growth was assigned a value of  $0.1 \text{ day}^{-1}$  at time  $t = 0$  (birth) based on experimental measurements (Comer, 1956) and decreases exponentially to a negligible value at time  $t = 5\tau$  representing maturation. The maximum specific rate of tendon growth at time  $t$  is therefore (in units of  $\text{day}^{-1}$ )

$$(\dot{L}_0)_t / (\dot{L}_0)_t^{\max} = 0.1 \exp(-t/\tau). \quad (3)$$

Because tendons can become slack during normal function (Narici et al., 1996), no changes in tendon length occur if the minimum tendon strain is negative.

The optimal muscle length changes at a rate proportional to the average muscle extension (Fig. 2). The maximum rate of change is fixed at 1.2 mm/day since this is the maximum rate at which the rat gastrocnemius grows (Comer, 1956) and the approximate rate at which bones can be lengthened with good muscle adaptation in both immature and mature animals (Simpson et al., 1995; Williams et al., 1999; Hayatsu and De Deyne, 2001).

Initial values for tendon slack length  $(L_0)_t$ , muscle optimal length  $(L_{\text{opt}})_m$ , and muscle zero length  $(L_0)_m$  are specified at a time  $t$  (Fig. 2). Muscle zero length represents the length beyond which passive tension occurs in the muscle. A constant muscle length offset is calculated as

$$\delta_m = (L_{\text{opt}})_m - (L_0)_m, \quad (4)$$

and a time increment  $\Delta t$  is applied such that  $t = t + \Delta t$ . Time histories of MTU length are specified so the minimum  $(L_{\text{min}})_{\text{MTU}}$ , maximum  $(L_{\text{max}})_{\text{MTU}}$ , and average  $(L_{\text{avg}})_{\text{MTU}}$  length are known at all times. The ratio of tendon stiffness to muscle stiffness  $(S_t/S_m)$  is also specified. MTU slack length is calculated as

$$(L_0)_{\text{MTU}} = (L_0)_t + (L_0)_m, \quad (5)$$

and MTU functional length is

$$(L_j)_{\text{MTU}} = (L_j)_t + (L_j)_m, \quad (6)$$

where  $j = \{\text{max, min, avg}\}$ . MTU displacement is then

$$(d_j)_{\text{MTU}} = (L_j)_{\text{MTU}} - (L_0)_{\text{MTU}}. \quad (7)$$

Tendon displacement is

$$(d_j)_t = (d_j)_{\text{MTU}} / (1 + S_t/S_m), \quad (8)$$

since the muscle and tendon share the same force  $F = S_t(d_j)_t = S_m(d_j)_m = S_m[(d_j)_{\text{MTU}} - (d_j)_t]$ . Muscle displacement is

$$(d_j)_m = (d_j)_{\text{MTU}} - (d_j)_t, \quad (9)$$

and average muscle length is

$$(L_{\text{avg}})_m = (L_0)_m + (d_{\text{avg}})_m. \quad (10)$$

The tendon adaptation rule determines the specific rate of change of tendon length  $(\dot{L}_0)_t / (L_0)_t$  using the minimum tendon strain  $(\epsilon_{\text{min}})_t = (d_{\text{min}})_t / (L_0)_t$ . The

muscle adaptation rule determines the rate of change of optimal muscle length  $(\dot{L}_{\text{opt}})_m$  using the average muscle extension  $(D_{\text{avg}})_m = (L_{\text{avg}})_m - (L_{\text{opt}})_m$ . These rates are used to update the tendon slack length

$$(L_0)_t(t) = (L_0)_t(t - \Delta t) + (\dot{L}_0)_t / (L_0)_t (L_0)_t(t - \Delta t) \Delta t \quad (11)$$

and muscle optimal length

$$(L_{\text{opt}})_m(t) = (L_{\text{opt}})_m(t - \Delta t) + (\dot{L}_{\text{opt}})_m \Delta t. \quad (12)$$

The updated muscle zero length is calculated as

$$(L_0)_m(t) = (L_{\text{opt}})_m(t) - \delta_m. \quad (13)$$

The model was used in four applications: normal development, bone lengthening, immobilization, and retinacular release (Table 1).

The first application simulated growth of the male rat gastrocnemius. A time constant of  $\tau = 22$  days was selected based on an exponential fit of bone growth rate data (Comer, 1956). Average MTU length is specified (in mm) as

$$(L_{\text{avg}})_{\text{MTU}} = -0.0066t^2 + 0.9078t + 8.097 \quad \text{if } t < 68 \text{ days}, \quad (14)$$

$$(L_{\text{avg}})_{\text{MTU}} = 39.3 \quad \text{if } t \geq 68 \text{ days}, \quad (15)$$

where  $t$  is the rat's age in days (Comer, 1956). The initial length at birth ( $t = 0$ ) was divided between muscle and tendon in proportion to their lengths at birth (Comer, 1956). Maximum and minimum MTU length were specified as

$$(L_{\text{max}})_{\text{MTU}} = 1.15(L_{\text{avg}})_{\text{MTU}} \quad (16)$$

and

$$(L_{\text{min}})_{\text{MTU}} = 0.85(L_{\text{avg}})_{\text{MTU}} \quad (17)$$

to approximate a 30% excursion of the muscle belly (Comer, 1956). Since the stiffness ratio  $S_t/S_m$  is unknown, a parametric study using different fixed ratios was conducted. Variable stiffness ratios were also investigated.

The second application simulated muscle and tendon adaptation during bone lengthening. It used the same inputs as the previous application with  $S_t/S_m = 0.5$  except that lengthening was simulated by increasing the average MTU length at a typical rate of 1 mm/day starting at age 30 days for immature rats and 90 days for mature rats. Lengthening continued until the average MTU length had increased 20%. Good muscle adaptation has been observed for bone lengthening at rates under 1.2 mm/day with lengthening up to 20% of limb length (Simpson et al., 1995; Williams et al., 1999; Hayatsu and De Deyne, 2001).

The third application simulated immobilization of the mouse soleus with the ankle in its most dorsiflexed and most plantarflexed positions. The same time constant and average MTU length were used. However, the maximum and minimum MTU lengths were adjusted to

Table 1

Simulation input parameters for normal development (rat gastrocnemius), bone lengthening (rat gastrocnemius), immobilization (mouse soleus), and retinacular release (rabbit tibialis anterior)

Parameter	Description	Value	Application	References
$\tau$	Time constant	22 days	Development Lengthening Immobilization	Comer (1956)
$(L_0)_t(0)$	Initial tendon slack length	2.6 mm	Development Lengthening Immobilization	Comer (1956)
$(L_0)_m(0)$	Initial muscle zero length	4.3 mm	Development Lengthening Immobilization	Comer (1956)
$(L_{opt})_m(0)$	Initial muscle optimal length	5.0 mm	Development Lengthening Immobilization	Comer (1956)
$S_t/S_m$	Stiffness ratio	Parametric study; results shown for $S_t/S_m = 0.5$ and variable $S_t/S_m$ (1.2 at $t = 0$ , decreasing by $0.04 \text{ day}^{-1}$ to 0.35)	Development	Herbert et al. (2002)
$S_t/S_m$	Stiffness ratio	0.5	Lengthening	Herbert et al. (2002)
$S_t/S_m$	Stiffness ratio	1	Immobilization	Herbert and Crosbie (1997)
$(L_{avg})_{MTU}$	Average MTU length	$-0.0066t^2 + 0.9078t + 8.097$ to peak, then constant	Development Immobilization	Comer (1956)
$(L_{min})_{MTU}$	Minimum MTU length	$0.85(L_{avg})_{MTU}$	Development	Comer (1956)
$(L_{max})_{MTU}$	Maximum MTU length	$1.15(L_{avg})_{MTU}$	Development	Comer (1956)
$(L_{avg})_{MTU}$ $(L_{min})_{MTU}$ $(L_{max})_{MTU}$	Average, minimum, maximum MTU length	Same as for normal development with $(L_{avg})_{MTU}$ increasing 1 mm/day starting at $t = 30, 90$ days	Lengthening	Simpson et al. (1995), Williams et al. (1999), Hayatsu and De Deyne (2001)
$(L_{avg})_{MTU}$	Average MTU length	Same as for normal development, but fixed at $0.85(L_{avg})_{MTU}$ for immobilization in the shortened position and $1.05(L_{avg})_{MTU}$ for immobilization in the lengthened position for 21 days starting at $t = 14, 90$ days	Immobilization	Williams and Goldspink (1978)
$(L_{min})_{MTU}$	Minimum MTU length	$0.85(L_{avg})_{MTU}$ from normal development, but fixed at $1.05(L_{avg})_{MTU}$ for immobilization in lengthened position for 21 days starting at $t = 14, 90$ days	Immobilization	Williams and Goldspink (1978)
$(L_{max})_{MTU}$	Maximum MTU length	$1.05(L_{avg})_{MTU}$ from normal development, but fixed at $0.85(L_{avg})_{MTU}$ for immobilization in shortened position for 21 days starting at $t = 14, 90$ days	Immobilization	Williams and Goldspink (1978)
$\tau$	Time constant	55 days	Release	Nakagawa et al. (1996)
$(L_0)_t(0)$	Initial tendon slack length	4.8 mm	Release	Alder et al. (1958)
$(L_0)_m(0)$	Initial muscle zero length	5.8 mm	Release	Alder et al. (1958)
$(L_{opt})_m(0)$	Initial muscle optimal length	10.0 mm	Release	Alder et al. (1958)
$S_t/S_m$	Stiffness ratio	1	Release	Herbert et al. (2002)
$(L_{max})_{MTU}$	Maximum MTU length	$-0.0054t^2 + 1.3095t + 40.5920$ to peak, then constant	Release	Alder et al. (1958)
$\Delta L_{MTU}$	MTU excursion	$(-0.0778 \ln(t) + 0.6978)(L_{max})_{MTU}$ normally, increased by 35% for release	Release	Alder et al. (1958)
$(L_{min})_{MTU}$	Minimum MTU length	$(L_{max})_{MTU} - \Delta L_{MTU}$	Release	
$(L_{avg})_{MTU}$	Average MTU length	$(L_{min})_{MTU} + 0.25 \Delta L_{MTU}$	Release	Williams and Goldspink (1978)

match the muscle's operating range. Minimum in vivo length (at full plantarflexion) is approximately 80% of maximum in vivo length (at full dorsiflexion), and the muscle generates maximal active tension at approximately 95% of its maximum in vivo length (Williams and Goldspink, 1978). Maximum MTU length was therefore set at

$$(L_{\max})_{\text{MTU}} = 1.05(L_{\text{avg}})_{\text{MTU}}, \quad (18)$$

and minimum MTU length was set at

$$(L_{\min})_{\text{MTU}} = 0.85(L_{\text{avg}})_{\text{MTU}}. \quad (19)$$

The maximum, minimum, and average MTU lengths were fixed at the normal MTU maximum length to simulate immobilization in the lengthened position. The lengths were fixed at the normal MTU minimum length to simulate immobilization in the shortened position. A constant stiffness ratio of  $S_t/S_m = 1$  was used since the rabbit soleus experiences similar muscle and tendon elongation (Herbert and Crosbie, 1997). Immobilization was imposed between ages 14–35 and 90–111 days to simulate 3 weeks of immobilization in young and adult animals.

The fourth application simulated experiments in which the rabbit tibialis anterior retinaculum is released so the tendon can “bowstring”. Normal MTU lengths for the fully plantarflexed position were expressed (in mm) as a function of the rabbit's age  $t$  (in days) as

$$(L_{\max})_{\text{MTU}} = -0.0054t^2 + 1.3095t + 40.592$$

if  $t < 121$  days,

$$(L_{\max})_{\text{MTU}} = 120.0 \quad \text{if } t \geq 121 \text{ days}, \quad (20)$$

using data from Alder et al. (1958). MTU excursion as a proportion of MTU maximum length was estimated as

$$\Delta L_{\text{MTU}} / (L_{\max})_{\text{MTU}} = -0.0778 \ln(t) + 0.6978 \quad (21)$$

during growth to age 120 days and held constant thereafter, with an excursion of 74% at time  $t = 0$ , based on data from Alder et al. (1958). Minimum MTU length was then calculated as

$$(L_{\min})_{\text{MTU}} = (L_{\max})_{\text{MTU}} - \Delta L_{\text{MTU}}, \quad (22)$$

and average MTU length was calculated as

$$(L_{\text{avg}})_{\text{MTU}} = (L_{\min})_{\text{MTU}} + 0.25 \Delta L_{\text{MTU}}, \quad (23)$$

assuming that function of the tibialis anterior is opposite to that of the soleus. The muscle and tendon were assigned initial lengths in proportion to their estimated lengths at birth (Alder et al., 1958). A stiffness ratio of  $S_t/S_m = 1$  was used since muscle and tendon elongation are of similar magnitude in the human tibialis anterior MTU (Herbert et al., 2002). Retinacular release was simulated by increasing the MTU excursion 35%, while maintaining the same MTU maximum length (Burkholder and Lieber, 1998; Koh and Herzog, 1998; Burkholder, 2001). The change in excursion was applied

starting at ages 14 and 120 days to simulate retinacular release in growing and adult animals.

### 3. Results

The results for normal development agreed qualitatively with experimental observations for constant stiffness ratios between approximately 0.3 and 3. Initially, both the muscle and tendon increase in length roughly in proportion to increases in MTU (and bone) length (Comer, 1956; Alder et al., 1958) (Fig. 3). Over time, tendon growth slows while muscle growth continues (Comer, 1956; Alder et al., 1958).

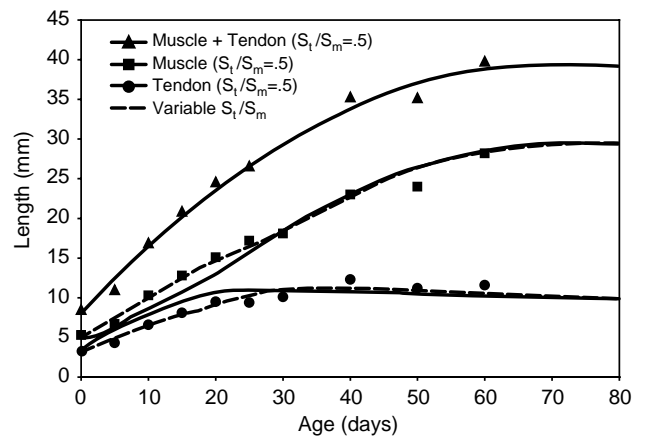


Fig. 3. Average muscle, tendon, and MTU lengths for normal growth of the rat gastrocnemius. Simulation results are shown for  $S_t/S_m = 0.5$  and for a variable  $S_t/S_m$  starting at 1.2 and decreasing by  $0.04 \text{ day}^{-1}$  to a final ratio of 0.35. Results are consistent with experimental data from

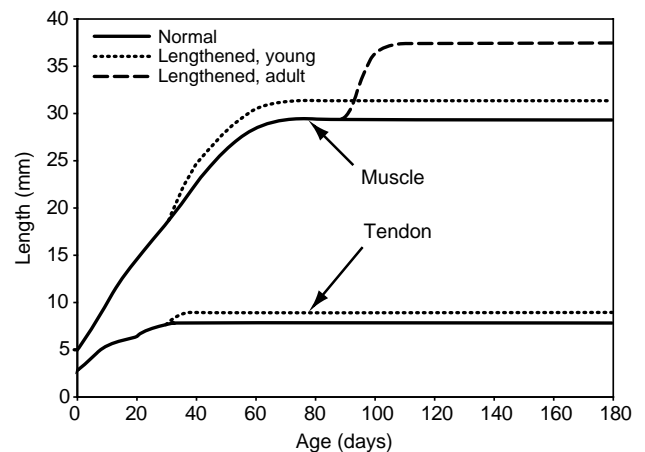


Fig. 4. Rat gastrocnemius muscle optimum length and tendon slack length during bone lengthening. Muscle length increases in both young and adult animals, but tendon length increases only in young animals. Results are consistent with experimental observations (Simpson et al., 1995; Fink et al., 1999; Williams et al., 1999).

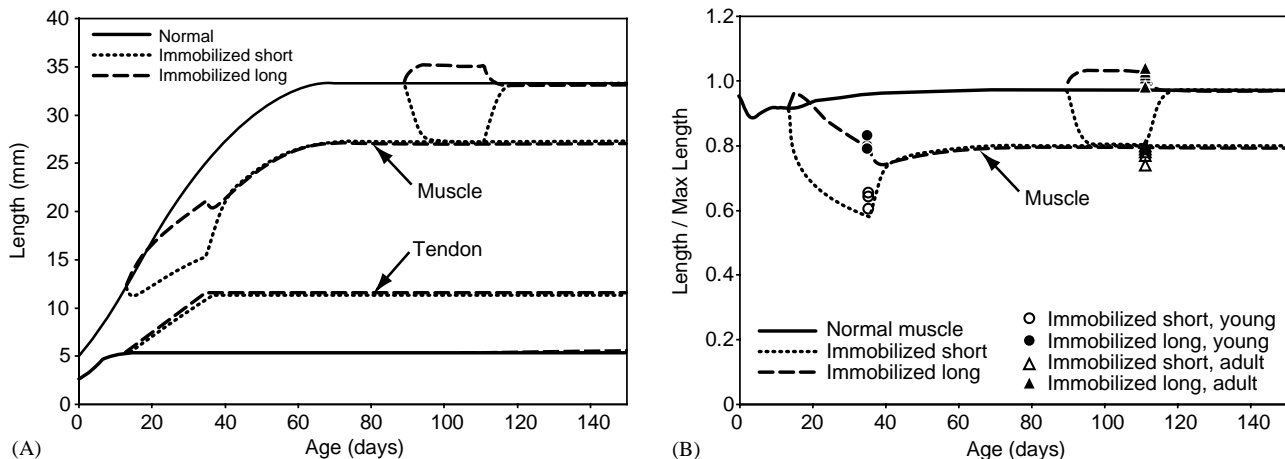


Fig. 5. Mouse soleus immobilization. (A) Muscle optimum length increases or decreases in adults depending on immobilization position, but decreases in young animals regardless of immobilization position. Tendon slack length increases in young animals regardless of immobilization position. (B) Muscle optimum length normalized by maximum muscle length. Results are consistent with experimental data from Williams and Goldspink (1978).

A constant stiffness ratio of 0.5 produced muscle and tendon growth similar to that reported by Comer (1956) (Fig. 3). This ratio seems reasonable for the rat gastrocnemius since muscle fascicle elongation accounts for 26% of the MTU elongation in human gastrocnemius MTUs (Herbert et al., 2002). The data can be even better approximated using a variable stiffness ratio (Fig. 3).

For bone lengthening, the simulation results predicted muscle length increases in both mature and immature animals (Fig. 4) consistent with experimental findings of increased serial sarcomere numbers following bone distraction (Simpson et al., 1995; Williams et al., 1999). For mature animals, the simulations predicted that the change in optimum muscle length approximates the magnitude of MTU lengthening, consistent with a shift in the muscle's active length–tension curve by the amount of lengthening (Simpson et al., 1995). In immature animals, the simulation results predicted increases in both muscle and tendon length. Fink et al. (1999) reported increases of 9–13 mm for various tendons during a 25 mm bone lengthening in young dogs. Muscle lengthening should account for the remainder of the bone length increase.

For immobilization of adult animals, the simulations predicted increased muscle optimum length for immobilization in the lengthened position and decreased muscle optimum length for immobilization in the shortened position (Fig. 5A), consistent with experimental observations of changes in serial sarcomere numbers (Tabary et al., 1972; Williams et al., 1998). With remobilization, muscle optimal length and sarcomere number rapidly return to normal (Tabary et al., 1972) (Fig. 5A). Tendon length does not change with immobilization in adult animals (Fig. 5A).

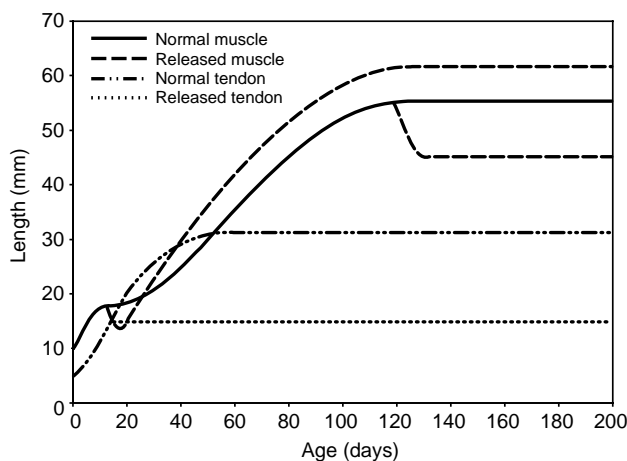


Fig. 6. Muscle optimum length and tendon slack length following release of rabbit tibialis anterior retinaculum. Results are consistent with experimental observations (Crawford, 1954; Burkholder and Lieber, 1998; Koh and Herzog, 1998; Burkholder, 2001).

For immobilization in growing animals, the simulations predicted decreases in muscle optimum length and increases in tendon length for immobilization in both lengthened and shortened positions (Fig. 5A), consistent with experimental observations (Williams and Goldspink, 1971, 1978). The magnitude of muscle optimum length change in the simulations agreed well with the experimental findings of Williams and Goldspink (1978) (Fig. 5B).

The simulation of retinacular release in growing animals predicted an 11% increase in optimal muscle length and a 15% decrease in tendon length (Fig. 6), consistent with the 14–22% increase in serial sarcomere number and 12–16% decrease in tendon length reported by Koh and Herzog (1998). The simulation also

predicted a 23% decrease in tendon length and a 14% increase in muscle length with the foot in its fully plantarflexed position, consistent with the 11–35% decrease in tendon length and 9–37% increase in muscle length reported by Crawford (1954) for the same foot position.

For retinacular release in adult animals, the simulation predicted no change in tendon length (Fig. 6), consistent with the experimental findings of Burkholder (2001). The decrease in MTU functional length was accommodated by a 19% decrease in muscle belly length (Fig. 6). Muscle length in full plantarflexion decreased 7%, consistent with the 8% decrease observed in adult mice (Burkholder and Lieber, 1998).

#### 4. Discussion

The model presented in this paper makes two primary contributions. First, it demonstrates that a single set of remodeling rules based on average muscle length and minimum tendon strain can describe muscle and tendon length adaptation in a variety of applications for both immature and mature animals. Previous investigators have generally assumed that immature and mature muscles respond differently to mechanical stimuli (Williams and Goldspink, 1973; Burkholder and Lieber, 1998; Koh and Herzog, 1998). This study suggests that the different results may derive from the same adaptation principles. Second, this study provides a theoretical and computational framework for understanding muscle and tendon length adaptation. This augments our previous understanding, which was based almost exclusively on experimental studies, and provides a foundation for future modeling of clinical applications.

This study follows the standard methods of computational mechanobiology and is subject to the limitations of this approach (van der Meulen and Huijkes, 2002). Perhaps most significant is the inability to “prove” that the model is valid. The best that can be done with this type of model is to show that it is consistent with experimental and clinical observations, as this study has done. Even this “reality check” has limitations since quantitative data are often not available for direct comparison with the simulation results. Additional experiments must be conducted to further validate and refine the model proposed in this study.

Another limitation is the need for quantitative parameter values. In this study, great effort went into selecting input parameters based on data from the literature. Nevertheless, the exact information required by the model was not always available, and the available data often appeared in a different form than needed. When appropriate data were not available, parametric studies were conducted to test model sensitivity to particular parameters.

A final limitation of the modeling approach is the lack of mechanistic detail in the model. Muscles change length through the addition and removal of sarcomeres in series within muscle fibers (Tabary et al., 1972; Williams and Goldspink, 1978; Simpson et al., 1995; Williams et al., 1999). Tendons change length through collagen remodeling (Tardieu et al., 1983). The proposed model is consistent with these mechanisms, but does not directly model them. Models like that of Humphrey (1999) work towards better representation of the mechanisms through which such adaptation occurs.

The current model is highly simplified. It uses a small strain formulation for tendon strain and does not account for details of the MTU length history. It does not specifically differentiate between postural and functional length. Consequently, the results do not indicate which length is more important for muscle adaptation.

A more general model would consider changes in cross-sectional and material properties as well as changes in length, with muscle and tendon stiffness included as output, rather than input, variables. Wren et al. (1998) presented a model in which peak cyclic strains regulate tendon cross-sectional area, modulus, and strength. Taber (1998) proposed another model in which passive stresses regulate muscle length, while active stresses regulate muscle cross-sectional area. This approach is conceptually consistent with the model proposed in the current study since muscle growth that reduces muscle extension would also reduce passive stresses.

The model presented in this paper was developed to improve our understanding of how muscles and tendons adapt to mechanical stimuli. The results suggest that tendons grow in response to minimum tensile strains, with the tendons' growth capacity diminishing with age, while muscles adapt throughout life in response to changes in their average length. These concepts may contribute to a better understanding of how muscle and tendon length insufficiencies develop as well as the ability to better predict the long-term outcome of interventions intended to alter muscle and tendon length.

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