A Novel Hill-type Two-mode Model of Skeletal Muscle to Simulate Mechanisms Underlying Position Control on the Descending Limb of the Force–Length Relation

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Abstract In a new Hill-type two-mode model of skeletal muscle, a stretch-evoked force enhancement mode is introduced in addition to a sliding filament mode on the descending limb of the isometric force–length relationship. Dynamic behaviors of muscle on the descending limb are examined in computer simulation using the model. First, force responses of the model to ramp-stretch of muscle are similar to those of frog semitendinosus muscle at different levels of muscle activation. Second, length–velocity phase trajectories of the model in isotonic tetanus contraction are similar to those of rabbit skeletal muscle. Third, firing rates of some motor units of human finger extensor muscle are slightly lower in static position control than in isometric contraction. Computer simulation is performed to reveal mechanisms underlying these behaviors. A hypothesis of static position control on the descending limb based on the simulation results is proposed; i.e., some active motor units of the finger extensor muscle operate in a stretch-evoked force enhancement mode, such that the stable finger position can be maintained owing to the spring-like property of these motor units.

Keywords: residual force enhancement, position control, firing rate, motor unit, computer simulation.

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1. Introduction

It is well known that the isometric force varies with the sarcomere length, or muscle length. The slope of the ascending limb (hereinafter referred to as the as-limb) of the force–length (stiffness) relationship is positive (Fig. 1). The muscle can operate as a spring-like actuator, such that the static length is easily controlled in a stable manner. Meanwhile, the slope of the descending limb (ds-limb) is negative; i.e., the muscle seems to be controlled in an unstable manner because of the negative stiffness. Recent studies showed that several human muscles operate on the ds-limb [1–3]. Although the control of an unstable system is difficult, humans control their limb movement easily. To the best knowledge of the author, few studies have focused on the mechanisms of position control on the ds-limb.

One of the most distinguishing properties of the ds-limb is residual force enhancement after stretch (rFE) [4]; i.e., the steady-state force exerted in the hold phase during a ramp-hold stretch is stronger than the isometric force exerted at the stretched length. The rFE phenomenon has been studied in various muscle preparations [5,6]. Edman [7] recently reported that non-uniform sarcomere
behavior and the recruitment of passive elastic elements (probably titin) are both likely to play an important role in rFE. On the basis of these physiological results, we refer to stretch-evoked force enhancement as ST-enhancement and assume that it occurs during and after stretching.

A mathematical model of skeletal muscle is useful to engineers and scientists interested in the neuromuscular control system and the design of functional electrical stimulation and prosthetic devices. While many models have been proposed [8–10], few reports have focused on properties on the ds-limb. In a previous paper, the author proposed a new Hill-type two-mode model comprising a sliding filament mode (SL-mode) and a stretch-evoked force enhancement mode (ST-mode) [11]. Note that ST-enhancement occurs in ST-mode. The model responses closely agreed with force transients obtained from frog muscle in tetanic contraction [12]. The model is used in the present study. For simplicity, the term "position control" is used not only for the position of the limb but also for the length of muscle in the present paper. “Position control” is static position control unless otherwise noted. The purpose of the present study is to clarify the mechanism underlying position control on the ds-limb utilizing the model.

First, a computer simulation is performed to explain force responses to stretch frog muscle at different levels of activation and to investigate the dependence of muscle activation on ST enhancement (section 4.1). The muscle activation-dependent property is used in section 4.3.2.

Second, computer simulation of the isotonic contraction of rabbit skeletal muscle is performed to examine stability of the muscle in SL-model of the ds-limb (section 4.2).

Third, firing rates of human motor units (MUs) in position control are compared with those in isometric contraction (subsection 4.3.1). Physiological data previously published are used [13].

Fourth, a computer simulation of the model is performed focusing on the difference in muscle activation (MU activity) to investigate the stability of muscle (subsection 4.3.2).

Finally, a hypothesis of position control of the ds-limb is proposed based on the results of these investigations (subsection 4.3.3).

2. Physiological findings for the force–length relation

The relationship between the isometric force and muscle length is shown schematically in Fig. 1 (curve i). The maximum isometric force Po is reached at the optimal length Lo. As the muscle length increases, the isometric force increases on the as-limb and decreases on the ds-limb. For simplicity, the plateau region around Lo is included on the ds-limb in this study. When the muscle is longer than a certain length around Lo, the passive force is usually developed by the connective tissues surrounding the muscle. The passive force–length relation in the relaxed state is nonlinear, as shown by curve r. The active force is obtained by subtracting the passive force from the measured force. The active force is used in the present study unless otherwise specified.

3. Mathematical model

3.1 Structure of a Hill-type two-mode model

The Hill-type model [14] is shown in Fig. 2A. The active force of the contractile component (CC) comes from the force generated by the actin and myosin cross-bridges at the sarcomere level. The series elastic component (SEC) represents the intrinsic elasticity of myofilaments and tendon. The passive component is ignored owing to its small effect in the present study.

3.2 Model in SL-mode

A model in SL-mode is shown in Fig. 2B [11]. For mathematical expression, the CC is represented by a force generator (FG) and a viscous-like component (VC). Mathematical expressions are as follows. The muscle length \( L(t) \) as a function of time \( t \) is given by

\[
L(t) = L_{CC}(t) + L_{SEC}(t),
\]

(1)

where \( L_{CC} \) is the length of the CC, and \( L_{SEC} \) is the length of SEC. The load (force) \( P \) is expressed as

\[ F = \text{force generator} \times L_{SEC} \]

Fig. 2  Hill-type two-mode model of muscle: (A) Hill-type model, (B) SL-mode, and (C) ST-mode. CC, contractile component; SEC, series elastic component; FG, force generator; VC, viscous-like component; PEC_{ST}, parallel elastic-like component.
where \( k_e \) is the elastic coefficient of the SEC and \( \Delta L_{SEC} \) is the extension of the SEC. We measure the force–load–velocity relations and obtain the following equations [15]:

\[
P(t) = F(t) + Bv(t),
\]

(3)

where \( F \) is the contractile force of the FG, \( B \) is the viscous-like coefficient of the VC, and \( v \) is the velocity. Note that \( F \) is a function of \( L \) and \( M_a \):

\[
F(t) = M_a(t)F_L(L),
\]

(5)

where \( F_L \) is the isometric force generated in tetanus contraction at the muscle length \( L \), while \( M_a \) is the muscle activation; \( M_a \) is 1.0 (100%) in tetanus contraction and zero in the resting state. For the shortening of muscle \( (v < 0) \), we obtain

\[
B = F(Po + a)/Po(-v + b),
\]

(6)

where \( a \) and \( b \) are constants (Appendix). Note that \( B \) varies with \( F \) and velocity \( v \). For the lengthening of muscle \( (v > 0) \), we obtain

\[
B = F(Po + a')/Po(v + b'),
\]

(7)

where \( a' \) and \( b' \) are constants (Appendix). The mass of the muscle is ignored because of its small effect on the developed force.

3.3 Model in ST-mode

A model in ST-mode is shown in Fig. 2C [11]. A parallel elastic-like component (PECST) is added to the CC. The transition between SL-mode and ST-mode occurs according to the following rules (Fig. 3).

(Rule 1) The mode changes from SL-mode to ST-mode when the contracting muscle in SL-mode on the ds-limb (\( L > L_o \)) is stretched \( (dL/dt > 0) \). The time of stretching is denoted by \( t_{ST} \) and the muscle length by \( L_{ST} \).

(Rule 2) The mode changes from ST-mode to SL-mode when the length becomes shorter than \( L_{ST} \); i.e., \( dL/\text{d}t < 0 \) and \( L < L_{ST} \).

In ST-mode, we have

\[
P(t) = F_{ST}(t) + Bv(t) + k_p(L_{cc}(t) - L_{CCST}),
\]

(8)

where \( F_{ST} \) is the contractile force of the FG, \( k_p \) is the elastic coefficient of PECST, and \( L_{CCST} \) is the length of the CC at \( t_{ST} \) \( (L_{CCST} = L_{CC}(t_{ST})) \). We assume that \( F_{ST} \) changes linearly with the muscle activation \( M_a \):

\[
F_{ST}(t) = F(t_{ST})M_a(t)/M_a(t_{ST}),
\]

(9)

where \( F(t_{ST}) \) is the contractile force \( F \) at \( t = t_{ST} \). The viscous-like coefficient of the VC is expressed by

\[
B = F_{ST}(Po + a)/Po(-v + b) \quad (v < 0),
\]

(10)

\[
B = F_{ST}(Po + a')/Po(v + b') \quad (v > 0).
\]

(11)

The Runge–Kutta method is adopted in the present computer simulation.

4. Results

4.1 Force response at different levels of activation

This section examines the dependence of the parameter \( k_p \) on the contractile force in ST-mode. Figure 4 shows time courses of the force response to the ramp-stretch of muscle (i.e., frog semitendinosus muscle, 10°C) [16]. In a computer simulation, force \( P(t) \) after the onset of stretch is calculated with Eqs. (1), (2), (4) and (8)–(11). \( L(t) \) is given as a ramp-hold function (Fig. 4) and \( F_{ST} \) is the steady isometric force at the onset of stretch. \( F_{ST} \) is 1.0Po, 0.75Po, and 0.4Po in Fig. 4A, B, and C, respectively. The model responses are shown as broken lines in Fig. 4. Close agreement is seen in the figure. The con-

![Fig. 3](image-url) Transition between the ST-mode and SL-mode, where \( t \) is time.

![Fig. 4](image-url) Simulation of the force response to the ramp-stretch of muscle (frog semitendinosus muscle, bundle of fibers at 10°C) when exerting a steady isometric force. Top trace is elongation of the muscle length. Lower trace is force: solid line, experimental result [16]; broken line, simulated curve. \( F_{ST} = 1.0Po \) in (A), \( F_{ST} = 0.75Po \) in (B), and \( F_{ST} = 0.4Po \) in (C); the velocity of stretch is about 4.0 mm/s, \( L_o = 14 \text{ mm}, Po = 0.053 \text{ N} \).
cants are \(a' = 0.4\), \(b' = 0.85Lo/s\), and \(k_s = 50.0Po/Lo\).
The coefficient \(k_p\) varies linearly with \(F_{ST}\):

\[
k_s = k_\infty F_{ST}/Po,
\]

where the constant \(k_\infty = 7.0Po/Lo\).

4.2 Isotonic contraction on the ds-limb

The previous report [11] indicated the instability of muscle in SL-mode on the ds-limb with a linearized model.
The length response (Laplace transform) to the stepwise change in load is given by

\[
L(s) = (b_1s + b_2)/s(s - b_3),
\]

where \(b_1\), \(b_2\), and \(b_3\) are positive constants. To support this result, time courses of the length change in isotonic tetanus contraction are computed using the nonlinear model in SL-mode [Eqs. (1)–(7)] and compared with physiological data of rabbit skeletal muscle [17]: the initial length is 1.17Lo (point S in Fig. 5) while the isotonic load is 0.2\(Po\) or 0.4\(Po\). The muscle activation \(M_a(t) = 1.0\) and the parameters \(k_s = 40Po/Lo\), \(a/Po = 0.36\), and \(b = 2.0Lo/s\) [17] are used in the simulation. The isometric force–length relation of cat muscle [18] is approximated with a straight line: \(F_L(L) = 0\) at \(L = 0.6Lo\), \(Po\) at 0.93\(Lo\), \(Po\) at 1.0\(Lo\), and 0 at 1.8\(Lo\).

Length–shortening velocity phase trajectories obtained in the simulation are shown in Fig. 5. The trajectories agree closely with physiological results (Figure 10 of [17]). Instability of the muscle on the ds-limb is shown by the behavior that the muscle continues to shorten against the isotonic load on the ds-limb.

4.3 Mechanism of static position control

4.3.1 MU activity

The methodology of the physiological experiment [13] was as follows. In force control (isometric contraction), the participant maintained an isometric force around the metacarpophalangeal joint at a given level for a few seconds. Trains of action potential of a single MU of the extensor digitorum communis (EDC) muscle were recorded with intramuscular bipolar fine wire electrodes. The mean firing rate of the MU was obtained by averaging instantaneous firing rates during a certain period. In position control, the participant maintained a constant middle-finger position against an applied force. The mean firing rate of the same MU was similarly calculated. In Fig. 6, firing rates in force control are plotted as open circles and those in position control as closed squares; these results are adopted from [13].

Linear regression analysis is applied to both controls. The results for position control (\(r = 0.98\)) are shown by a solid line while those of force control (\(r = 0.97\)) are shown by a broken line in Fig. 6. The figure shows that firing rates in position control are slightly lower than those in force control, when the force is in the approximate range of 1–2.2 N (10%–22% of the maximum isometric voluntary contraction). Additionally, four MUs similarly have lower firing rates in position control than in force control, although the difference is not significant. Note that records of the finger movement obtained by eye [13] reveal that the MU in Fig. 6 is likely to be in ST-mode in position control. Each record shows that the contracting muscle is stretched by the electric motor and then maintained at the desired position by the participant.

4.3.2 Model analysis

Considering the difference in MU activity between force control (i.e., isometric contraction) and position control, length changes due to a small perturbation of muscle activation are calculated for two cases. In the first case (Fig. 7A), the operating point Q is on the isometric force–length relation of the SL-mode. In the second case (Fig. 7B), Q is on the force–length relation of the ST-
mode. The first case is referred to as the iSL-case and the second case as the iST-case. The two cases have the same initial conditions in that the muscle is maintained at the same equilibrium point Q, the muscle length Lq is the same, and the applied load P_L is the same. Parameters and conditions for the simulation are as follows.

(s-1) \( L_q = 1.1L_0 \) and \( P_L = 0.2P_0 \).

(s-2) The isometric force–length relation on the ds-limb is approximated with a straight line: \( F = P_0 \) at \( L = 1.0L_0 \) and \( F = 0 \) at \( 1.5L_0 \) of human muscle in tetanus [18].

(s-3) \( B \) is approximated as

\[
B = (F/P_0)Bo \quad \text{(iSL-case)},
\]

\[
B = (F_{ST}/P_0)Bo \quad \text{(iST-case)},
\]

where \( Bo \) is a constant because the velocity \( v \) is low in the simulation.

(s-4) \( k_s = 33P_0/L_0, k_{ps} = 15P_0/L_0, B_0 = 1.07P_0/(L_0/s) \); these values are based on estimations of parameters for the human flexor pollicis longus muscle [19].

Terms (s-1)–(s-4) are used in both cases. Terms (s-5) and (s-6) shown below are used in the iSL-case.

(s-5) The initial value of \( M_a \) is 0.25 (25%).

(s-6) The perturbation of \( M_a \) at \( t \geq 0 \) is

\[
M_a(t) = 0.25(1 + 0.02Sn(t)), \tag{15}
\]

\[
Sn(t) = \sum_{i=1}^{4} \sin 2\pi f_i t, \tag{16}
\]

where \( Sn \) is the sum of four sinusoidal waves and \( f_i = \{11, 17, 20, 27\} \) Hz. Both amplitudes and frequency are decided arbitrarily but considering physiological tremor.

Terms (s-7)–(s-9) shown below are used in the iST-case.

(s-7) \( L_{ST} = 1.08L_0 \).

(s-8) The initial value of \( M_a \) is 0.18 (18%).

(s-9) The perturbation of \( M_a \) at \( t \geq 0 \) is

\[
M_a(t) = 0.18(1 + 0.02Sn(t)) \quad (t \geq 0). \tag{17}
\]

Results of computer simulation in the iSL-case are shown in Fig. 8A. A small fluctuation of \( M_a \) (Fig. 8A middle trace) gives rise to a gradual shortening of the muscle length (top trace) where repetitive mode changes occur between the SL-mode and ST mode (bottom trace). The muscle length is not maintained at the initial length and gradually shortens with time. This indicates instability of the muscle. Results of computer simulation for the iST-case are shown in Fig. 8B. It is seen that the muscle is stable against a perturbation of muscle activation.

### 4.3.3 Hypothesis of position control

In isometric contraction, the level of muscle activation \( M_a \) is taken as 0.25 to meet the conditions \( L_q = 1.1L_0 \) and \( P_L = 0.2P_0 \) (i.e., the operating point Q in Fig. 7A). Meanwhile, \( M_a \) is 0.18 in the iST-case to meet the same conditions (Fig. 7B). A stable position is maintained in the iST-case as shown in Fig. 8B. It is assumed that these two conditions of muscle contraction correspond to force control and position control in Fig. 6; i.e., isometric contraction corresponds to force control while contraction in the iST-case corresponds to position control. The lower level of muscle activation corresponds to a lower firing rate of the MU. As a result, the computer simulation likely explains the physiological result that the firing rate in position control is lower than that in force control. Furthermore, it demonstrates that the muscle itself is stable in ST-mode against a disturbance without any feedback system (Fig. 8B).

A skeletal muscle comprises many MUs. Physiological data indicate that some MUs of EDC muscle have lower firing rates in position control than in force control while some MUs do not [13]. The operation of active MUs is not necessarily in ST-mode in position control. However, if some MUs operate in ST-mode, stiffness of the muscle around the operating point can become posi-
tive; i.e., stable position control is possible. On this basis, the author proposes a hypothesis of position control on the ds-limb; i.e., some active MUs of the finger extensor muscle are operating in ST-mode, such that a stable finger position can be maintained owing to the spring-like property of these MUs.

5. Discussion

5.1 Basis of motor control
In the neuromuscular control system, there are two fundamental types of control; namely, force control and position control [20]. Force control has been widely examined in voluntary isometric contraction. With respect to the mechanism of position control, a spring-like property of the muscle has been used [21]. In fact, such a property has been obtained for human elbow extensor muscles [22] while negative stiffness has been found for human elbow flexor muscle [23]. Human EDC muscle seems to have negative stiffness, because the physiological range is likely on the ds-limb. Negative stiffness of the actuator means an unstable control system. It is generally difficult to control an unstable system. However, people are able to control their limb position easily. No report can be found, which fully elucidates mechanisms of position control while considering the mechanical properties of muscle on the ds-limb. The present study may clarify the basis of position control.

5.2 Effect of muscle activation on ST-enhancement
Most muscle experiments have been performed for tenuus contraction. The present study shows that the coefficient of PECST, \( k_p \), is not constant but increases almost linearly with muscle activation. This result is important in that the model may be applied to examining behaviors of the muscle that change the level of muscle activation with time.

5.3 Neural activity in position control
This study shows that firing rates of single MUs of human EDC muscle are lower in position control than in force control. The same result was reported for 32 MUs of biceps brachii muscle of 15 healthy participants [24]. More physiological data for human muscle are required because the present physiological data seem to provide insufficient evidence.

Stretch reflex can be considered to play an important role in static position control. While the stretch reflex has been found for some MUs of EDC muscle, the force increase attributed to the short latency reflex has been insufficient [13]. The reflex loop has a neural delay, and a large gain of the feedback (i.e., stretch reflex gain) may destabilize the system. The stiffness of EDC muscle has no latency, and this seems important in maintaining a stable position of the metacarpophalangeal joint.

5.4 Assumptions made in the simulation
Several assumptions were made to make the first approximation. First, the residual force depression (rFD) [25] was not included. The rFD is a decrease in the steady isometric force following active shortening, compared with a reference isometric contraction for the same muscle length. Since rFD is not large when the shortening is small [11,12], it was therefore not included in the simulation. Second, the elastic coefficient \( k_p \) was assumed to depend only on muscle activation even though it may depend on the velocity of stretch [12] and the muscle length at the onset of stretch, \( L_{st} \) [5]. These factors must be considered if more precise simulation is required. Third, Rule 2 in section 3.3 was assumed without physiological evidence. Elaborate physiological experiments are required for further investigation.

5.5 Schematic model of skeletal muscle
Muscle has been represented as a rack–pinion mechanism (CC) and SEC [21]. The change in limb position is explained with this model. Although the rack–pinion mechanism is simple and useful in terms of showing changes in muscle length due to filament sliding, it does not provide an easy explanation of the equilibrium point of the muscle length. This is because the rack–pinion mechanism is rigid and not a force generator. The movement is similar to that of a stepping motor in that the motor converts digital pulses into mechanical shaft rotation (i.e., a motor position) and the motor may not rotate continuously but rather step from one position to the next. It is thus difficult to explain the position control of a muscle with a rack–pinion mechanism and SEC.

The author proposes a new schematic model of the muscle in a simplified form (Fig. 2). The model of the as-limb is presented in Fig. 9A, where M denotes an active site (i.e., cross-bridge). As the muscle lengthens, the CC force increases with an increasing number of active sites. This relation is similar to that of a spring. The active site M obeys the force–load–velocity relation. The model of the SL-mode on the ds-limb is presented in Fig. 9B, where movement is in the one direction of shortening. When the muscle shortens, the CC force increases with an increasing number of active sites. There is no spring within the CC. The model of the ST-mode on the ds-limb is presented in Fig. 9C, where a virtual spring PECST exists within the CC. The elastic coefficient of PECST increases with an increasing number of active sites. Note that the number of active sites does not change with variation of the muscle length.
6. Conclusion

Transient length changes and mechanisms underlying static position control on the ds-limb were simulated with a new Hill-type two-mode model of muscle.

Conflict of Interest

The author declares no conflicts of interest with any companies or commercial organizations per the definition of the Japanese Society for Medical and Biological Engineering.

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Appendix

We obtained a generalized form of Hill’s equation for a muscle generating the contractile force \( F(F \leq P_0) \) [15];
\[
(P + A)(v^* + b) = b(F + A) \tag{A-1}
\]
\[
A = a(F/P_0) \tag{A-2}
\]
where \( v^* \) is the shortening velocity, and Hill’s equation is obtained at \( F/P_0 = 1 \). Then, the load \( P \) is given by
\[
P = (bF - Av^*)/(v^* + b) \tag{A-3}
\]
Consequently, velocity dependent force loss given by \( F-P \) is
\[
F - P = F(Po + a)v^*/Po(v^* + b), \tag{A-4}
\]
When the lengthening velocity is denoted by \( v \) (i.e., \( v = -v^* \)), Eq. (A-4) is represented by
\[
P = F + Bv \tag{3}
\]
\[
B = F(Po + a)/Po(-v + b) \tag{6}
\]
For the lengthening of muscle, we obtained the generalized force-load-velocity relation [15]
\[
(P - 2F - A')(v^* - b') = b'(F + A') \tag{A-5}
\]
\[
A' = a'(F/P_0) \tag{A-6}
\]
Because \( v = -v^* \), the load \( P \) is given by
\[
P = (2Fv + Fb' + A'v)/(v + b') \tag{A-7}
\]
Then, we obtained the viscous-like coefficient \( B \) of Eq. (3) as
\[
B = F(Po + a')/Po(v + b') \tag{7}
\]

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