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Muscle contraction history: modified Hill versus an exponential decay model

Gertjan J. C. Ettema[1,2], **Kenneth Meijer**[3]

[1] Department of Anatomical Sciences, The University of Queensland, Australia
[2] Department of Sport Sciences, Norwegian University of Science and Technology, 7034 Trondheim, Norway
[3] Department of Integrative Biology, VLSB 3060, UC Berkeley, Berkeley, CA 94720-3140, USA

Abstract. In recent years, it has been recognised that improvements to classic models of muscle mechanical behaviour are often necessary for properly modelling co-ordinated multi-joint actions. In this respect, the purpose of the present study was to improve on modelling stretch-induced force enhancement and shortening-induced force depression of muscle contraction. For this purpose, two models were used: a modified Hill model and a model based loosely on mechano-chemistry of the cross-bridge cycle (exponential decay model). The models were compared with a classic Hill model and experimental data. Parameter values were based, as much as possible, on experimental findings in the literature, and tested with new experiments on the gastrocnemius of the rat. Both models describe many features of slow-ramp movements well during short contractions (300–500 ms), but long-duration behaviour is described only partly. The exponential decay model does not incorporate a force–velocity curve. Therefore, its good performance indicates that the status of the classic force–velocity characteristic may have to be reconsidered. Like movement-induced force depression and enhancement, it seems a particular manifestation of time-dependent force behaviour of muscle, rather than a fundamental property of muscle (like the length–tension curve). It is argued that a combination of the exponential decay model (or other models based on the mechano-chemistry of contraction) and structurally based models may be fruitful in explaining this time-dependent contraction behaviour. Furthermore, not in the least because of its relative simplicity, the exponential decay model may prove more suitable for modelling multi-joint movements than the Hill model.

1 Introduction

Modelling intrinsic properties of skeletal muscle-tendon units in the scope of co-ordinated movements has gained momentum in recent years (see Winters and Woo 1990; Beek 1991; Bobbert 1991; Otten 1991; Winters 1995; Huijing 1995; Herzog 1998a,b). With regard to the integrated function of motor behaviour, the neural system and mechanical actuators (muscles) rely heavily on each other's properties as well as their organisation. Thus, a proper understanding of the physiological and structural properties of skeletal muscle is essential to understand motor control and organisation (e.g. van Soest and Bobbert 1993; van Ingen Schenau et al. 1995; Winters 1995). Although many structural and biophysical models have been developed (see Zahalak 1990), in motor control studies the phenomenological modelling approach (based on Hill 1938) has prevailed, be it mainly for high-intensity tasks (see Winters 1995).

Irrespective of the modelling approach used, a strong need for model improvements on many aspects is apparent in the field of motor behaviour (see Huijing 1995; Winters 1995 for reviews). Two underdeveloped aspects are the phenomena of stretch-induced force enhancement (e.g. Ettema et al. 1990a,b, 1992; Edman et al. 1978; Herzog 1998b) and shortening-induced force depression (e.g. Edman 1975, 1980; Granzier and Pollack 1989; Herzog and Leonard 1996; Meijer et al. 1997, 1998; Herzog 1998b). These phenomena are usually referred to as 'history of contraction' and cannot always be ignored in muscle modelling in the scope of motor behaviour (van Ingen Schenau et al. 1988). Furthermore, these phenomena have been demonstrated in human activities (Walshe et al. 1998; de Ruiter et al. 1998; Lee et al. 1999).

In the present study, three models were compared. Two models were developed within the classic Hill paradigm, one representing the classic Hill model itself, the other forming an extension on the model presented by Meijer et al. (1998). A third phenomenological model was based loosely on a model described by Kawai and Brandt (1980), who attempted to describe the mechano-

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Correspondence to: G. J. C. Ettema
(Tel.: +47-73590616, Fax: +47-73591770,
e-mail: gertjan.ettema@svt.ntnu.no)

chemical coupling of the cross-bridge cycle. The comparison of the three models and experimental results aided in understanding of contraction dynamics as well as in the search of fruitful modelling of muscle actuator systems. Within this context, the specific aim was to understand the origin of the history of contraction with regard to the effects of stretch and shortening on subsequent isometric force production.

2 Methods

2.1 Simulation models

Three muscle models were studied, the classic Hill model (H), a modified Hill model (MH), and a model referred to as the exponential decay (ED) model. The ED model does not incorporate Hill's force–velocity relationship, but it describes the dynamics of muscle contraction using exponential functions, and as such may be loosely related to the biochemical reactions between actin and myosin leading to force production (see below, and Kawai and Brandt 1980).

All models (Fig. 1) were run in Matlab–Simulink (The MathWorks) using Gear's predictor-corrector method. The muscle consisted of three elements: contractile (CE), series elastic (SEE) and parallel elastic (PEE). The effects of PEE, i.e. passive muscle forces, were not of particular interest in this study. Thus, this element was not incorporated in the iterative solution, but simply calculated as a function of muscle-tendon complex length (l_{m}) and added to contractile element force. The input to the models consisted of two time traces: muscle-tendon complex length and active state (Q). The active state was derived from the binary stimulation pulse train using first-order dynamics (Hatze 1981).

2.2 H model

The length–tension properties of the elements are described by the following equations (the experimental data and fitting results are shown in Fig. 1D):

$$\text{SEE: } F_{\mathrm{see}} = s(l_{\mathrm{see}} - lo_{\mathrm{see}})^{u} \qquad (1)$$

$$\text{PEE: } F_{\mathrm{pee}} = pe^{(\mathrm{r} \times l_{\mathrm{m}})} + v l_{\mathrm{m}}^{w} \qquad (2)$$

$$\text{CE: } Fi_{\mathrm{ce}} = r_0 + r_1 l_{\mathrm{ce}} + r_2 l_{\mathrm{ce}}^2 + r_3 l_{\mathrm{ce}}^3 + r_4 l_{\mathrm{ce}}^4 \qquad (3)$$

where 'v' refers to velocity, 'i' refers to isometric force, 'o' refers to optimum (CE) and rest length (PEE and SEE), l_{ce} and l_{see} are the length of CE and SEE, respectively. The parameters $s, u, p, w, r_0, r_1, r_2, r_3$ and r_4 are fitting constants. The force–velocity relationship of the contractile element was only modelled explicitly in the H and MH models.

$$Fv_{\mathrm{ce}} = a_{\mathrm{j}}(b_{\mathrm{j}} + v_{\mathrm{ce}})^{-1} + c_{\mathrm{j}}; \qquad (4)$$
$$\mathrm{j} = \mathrm{ec}\colon v_{\mathrm{ce}} > v_{\tau}, \quad \mathrm{j} = \mathrm{co}\colon v_{\mathrm{ce}} < v_{\tau}$$

where Fv is the force as a function of velocity (as distinct from Fi). The parameters a_{j}, b_{j} and c_{j} are fitting constants. Equation (4) is not formulated according to the classic Hill denotation for the following reason. The transition velocity (v_{τ}) was used to allow expression of quantitative differences between concentric (co) and eccentric (ec) parts of the force–velocity curve. The value was determined by curve-fitting procedures and was always on close to, but not necessarily exactly, zero (isometric point). The constants in (1–4) were determined by curve fitting procedures, based on experimental data (see Sect. 3 for details). These equations were chosen mainly for pragmatic reasons; the functions are relatively simple and fitted the experimental data well.

2.3 MH model

Additional to the description of the H model, the MH model contained an extra element describing the contraction history effect (ΔFh_{ce}) that was based on literature information. First, the effects of force depression due to shortening and force enhancement due to stretch were distinguished as two different processes with different constants (and not merely as the reversed parts of a single process). Meijer et al. (1998) described the following aspects of force depression: the ratio of force depression and amplitude of shortening depends linearly on relative muscle length and exponentially on the velocity of shortening. Ettema et al. (1992) showed that a similar dependence occurred for force enhancement, but to a different (quantitative) extent. All dependencies are positive, i.e. the history effects are stronger at large muscle lengths and at high (positive) velocities. As shortening is defined as negative, the history effect (force depression) is reduced at high shortening velocities (Herzog and Leonard 1996; Meijer et al. 1997, 1998).

Two different influences need to be distinguished with respect to length- and velocity-dependent effects: (a) muscle length and velocity at the moment that contraction history is induced ('induction dependence'), i.e. at the time when the length change that brings about the history effect occurs; and (b) the muscle length and velocity at the moment that the history is effectuated and observed ('effectuation dependence'), i.e. at the time of measurement. For example, during a stretch-shortening contraction, the stretch induces a history effect that is maintained throughout the shortening period, during which it is measured as a deviation from Hill model predictions. The induction dependence indicates that the magnitude of history effects depends on the length and velocity during the stretch period. On the other hand, the effectuation dependence indicates that this magnitude depends on the actual length and velocity during the shortening period. It was shown for force depression and enhancement that the length-dependent influences were of the 'effectuation' type (Ettema et al. 1992; Meijer et al. 1998). The dependence of force enhancement on velocity was also an 'effectuation' dependence: in a stretch-shortening contraction, the stretch-induced enhancement during the shortening phase depends on

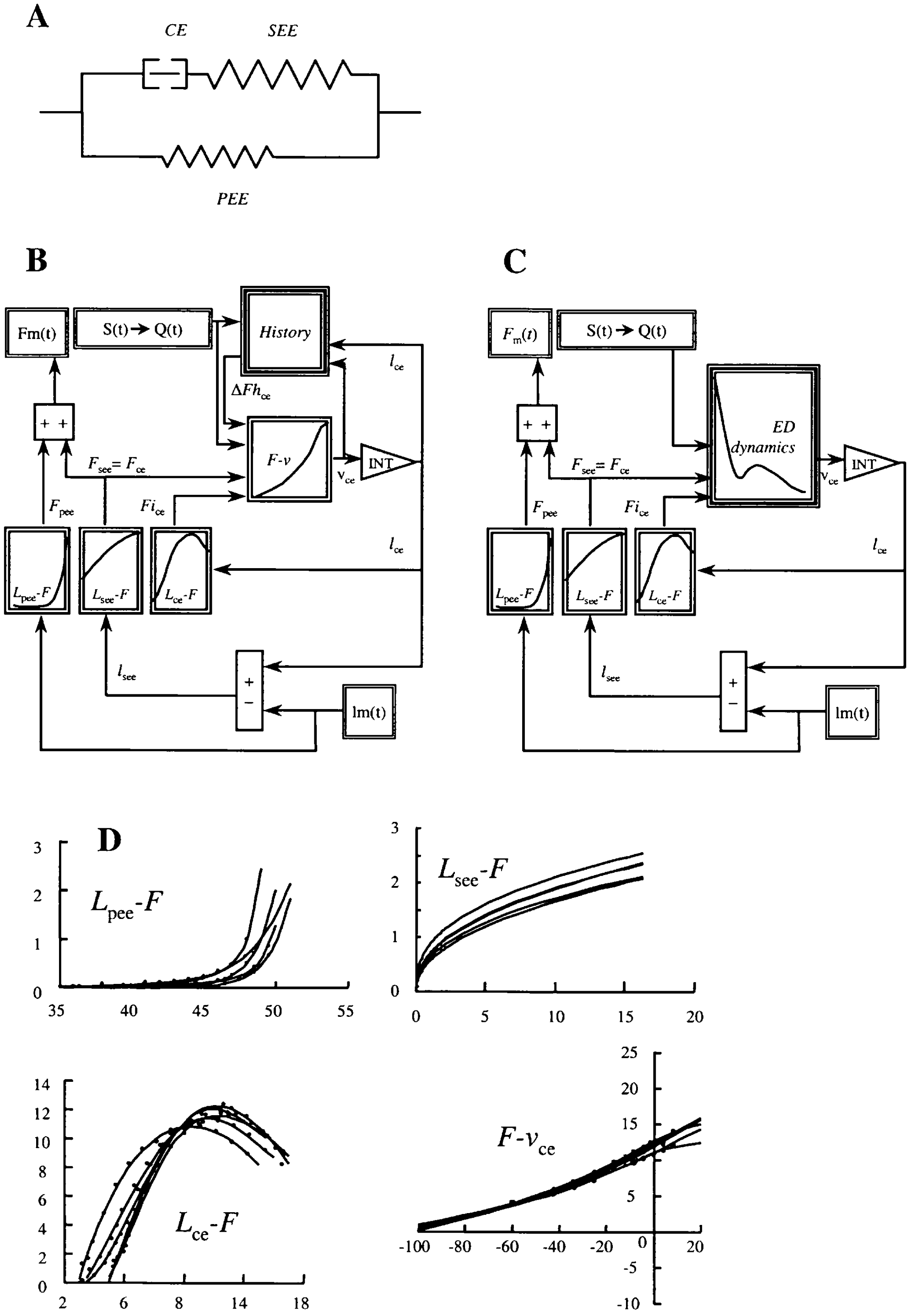

Fig. 1. **A** The Hill-type muscle model, consisting of three elements: contractile element (*CE*), series elastic element (*SEE*), and parallel elastic element (*PEE*). **B** Computer simulation of the modified Hill model, incorporating history effects (Eqs. 5–7) and properties of the three elements (Eqs. 1–4), symbolised by the curves in the four double-lined boxes. The classic Hill model is the same but without the '*History*' block. The inputs of the model are muscle length and stimulation pulse train [$S(t)$], transformed to active state as function of time [$l_m(t)$ and $Q(t)$]. **C** The exponential decay model, which is similar to the modified Hill model except for the replacement of the '*History*' and '*F-v*' boxes with the '*ED dynamics*' box (Eq. 8). **D** Basic characteristics of *PEE*, *SEE* and *CE* as measured (*symbols*) and fitted (*lines*) by (1–4) (n = 5). Measured data for SEE properties are not shown, as the force–extension curves are the integration of measured compliance values

the shortening velocity of that shortening period and not on the velocity of stretch that induced the history effect (Ettema et al. 1990b, 1992). The velocity dependence of force depression was of an 'induction' type. However, during the development of the present model, it was found that the dependence of force depression on shortening velocity most likely also contained an 'effectuation' component. Without incorporating such dependence, it was impossible to predict muscle force correctly during isokinetic shortening as well as during the isometric period subsequent to shortening. It should be noted here that the experiments by Meijer et al. (1998) and Herzog and Leonard (1996) clearly demonstrated the 'induction' dependence, but were not designed to verify or reject the 'effectuation' dependence of force depression on velocity. It was further assumed that the history effect decreases with time (see Winters 1995). Thus, the following equations were obtained describing the history effect (ΔFh_{ce}):

$$\Delta Fh_{ce}(t) = QH\gamma_{j,re}[(Q\gamma_{j,in}\Delta l_{ce}(t)) + R_t] \cdot e^{(T_j dt)}; \; j = \text{ec, co} \tag{5}$$

$$R_{\mathrm{t}} = [(Q\gamma_{\mathrm{j,in}}\Delta l_{\mathrm{ce}}(t)) + R_{\mathrm{t-1}}] \cdot \mathrm{e}^{(T_{\mathrm{j}}\mathrm{dt})} \tag{5a}$$

$$H_{\mathrm{j}} = f_{\mathrm{j}} l_{\mathrm{ce}} + h_{\mathrm{j}}; \;\; \mathrm{j=ec,\ co} \tag{6}$$

$$\gamma_{\mathrm{j,k}} = \mathrm{e}^{(\mathrm{g}_{\mathrm{j,k}} v_{\mathrm{ce}})}; \;\; \mathrm{j=ec,co;\ \ k = ef,\ in} \tag{7}$$

where ‘in’ refers to ‘induction’ and ‘ef’ to ‘effectuation’. T_{j} is a time constant; $f_{\mathrm{j}}, h_{\mathrm{j}}$ and $g_{\mathrm{j,k}}$ are constants (see Table 1).

Equation (5) is similar to an ordinary exponential equation (y = $a\mathrm{e}^{Tt}$), but allows accumulation of the effects of separate length changes in time. Thus, at induction, the magnitude of ΔFh depends on v_{ce} and Q. The effects of each length change accumulate with time, and further depend on Q, l_{ce} and v_{ce} at the time of effectuation (and measurement).

Most of the contraction history parameters were derived from the literature and were normalised for optimum CE length (lo_{ce}) and maximum isometric force (F_{o}). The time constants were estimated by performing a simulation of a single eccentric isokinetic stretch contraction with an isometric after-phase (see Sect. 3). The criterion for finding the best estimate for T_{ec} was to minimise the difference between the normalised force traces of both simulation and experimental traces. Normalised traces were used because at this stage the aim was not to simulate the magnitude of any effect, but merely its time dependence. A similar approach was used for T_{co}, but an isometric contraction was used rather than a concentric isokinetic contraction. The reason for this was that during isometric force build-up the CE is shortening to a significant extent, meaning that during concentric contractions the CE is actually shortening for most of the contraction period in a non-linear fashion. The initial force rise and, more importantly, the subsequent slow creep during the ‘force plateau’ of an isometric contraction were simulated. The time trace of the force creep was used as the criterion, as it could be assumed that Q had approached the maximum level (i.e. unity), ruling out any serious error by incorrectly describing $Q(t)$ in the simulation. This procedure was repeated for a number of contractions, resulting in T values that were of reasonable similarity. The average of the T values was used for further simulations. Furthermore, these values were used to correct the parameters taken from the literature, as the time of measurement of history effects is usually delayed relative to the moment of initiation.

Table 1 shows the normalised parameters, sources, and corrected values. All parameters are derived from rat gastrocnemius muscle experiments. The advantage of taking as many parameters as possible from the literature is that these values are independent of the experiments that are to be simulated. This approach was not used for the properties described in (1–4), as the aim of the study was to examine contraction history effects. Thus, any inaccuracy of the simulation in describing muscle behaviour could be attributed exclusively to an error regarding contraction history (i.e. incorrect reasoning or inaccuracy in the parameter estimation).

2.4 ED model

Kawai and Brandt (1980) described muscle behaviour over a range of frequencies by a third-order linear model. In rewritten form their Equation (5) is:

$$\Delta F = \xi_{\mathrm{co,\ ce}}(D + C\mathrm{e}^{ct} + B\mathrm{e}^{bt} + A\mathrm{e}^{at})\delta l \tag{8}$$

where A, B, C and D are constants, a, b, and c are time constants and δ is a gain factor (see Table 2 and text below). Equation (8) describes all rate-dependent contractile behaviour with three frequency-exponential components. Thus, apart from the isometric length–force characteristics, muscle force depends on length change, with the effect of each length step decaying exponentially with time. In the ED model, any particular force–velocity curve is an outcome of this length change time dependence, rather than a fundamental characteristic in itself. Furthermore, ‘contraction history’ (as described earlier) has become an integral part of the time dependent CE behaviour. It has been argued that the three exponential components reflect the mechanochemical rate processes in the cross-bridge cycle (Kawai and Brandt 1980; Kawai 1982; Calancie and Stein 1987).

Table 1. Values of constants describing the contraction history as formulated in (5–7). Corrections: (I) Q was estimated to be 0.9 as stretch occurred during onset of contraction; (II) T_{co}, t = 0.41; (III) T_{ec}, t = 0.25; (II and III) $x' = x\mathrm{e}^{(-T\,\mathrm{d}t)}$; (IV) by fitting literature data; (V) The $\mathrm{g}_{\text{co-ef}}$ value is derived by optimising the simulation of an experimental contraction (isokinetic shortening at −42.1 mm s^{-1} for a single experiment). The effect of $\mathrm{g}_{\text{co-ef}}$ on the isometric after phase is nil (at $v = 0, \gamma = 1$), but it allows a better fit during shortening given $\mathrm{g}_{\text{co-in}}$. Normalised values on basis of F_{o} and lo_{ce} if known, otherwise fibre length. * l_{ce} was estimated from rat size and unpublished lo_{ce} – rat mass data

Constant	Source	Normalised value	Corrected value	Method and correction
f_{ec}	Ettema et al. (1992)	5.055	24.00	I, III
h_{ec}	Ettema et al. (1992)	0.984	4.671	I, III
f_{co}	Meijer et al. (1998)	0.813*	1.854	I, II
h_{co}	Meijer et al. (1998)	0.614*	1.401	I, II
$\mathrm{g}_{\text{ec-ef}}$	Ettema et al. (1992) – this study	0.12	0.12	IV
$\mathrm{g}_{\text{ec-in}}$	Ettema et al. (1990b)	0	0	
$\mathrm{g}_{\text{co-ef}}$	Meijer et al. (1998) – this study	0.410	0.410	V
$\mathrm{g}_{\text{co-in}}$	Meijer et al. (1998) – this study	0.288*	0.288	IV
T_{ec}	This study	−6.23	−6.23	
T_{co}	This study	−2.00	−2.00	

Table 2. Values of constants describing the contraction history as formulated in (8). Sources: i = Kawai and Brandt 1980; ii = this study; iii = by default. Normalised values on basis of F_o and lo_{ce} if known, otherwise fibre length

Constant	Source	Normalised value	Constant	Source	Normalised value
C	i, ii	5.1	c	i	−526.5
B	i, ii	−1.56	b	i	−137.6
A	i, ii	0.67	a	i	−5.47
D	ii	250	ξ_{co}	iii	1
			ξ_{ec}	ii	7

The factor D represents the linear elastic modulus at 0 Hz (Kawai and Brandt 1980). This constitutes a permanent, non-decaying component of length-change effects, and should not be mistaken for the length–tension curve (Eq. 3) that regards length per se, not length change. It should be noted that the model by Kawai and Brandt (1980) is based on small amplitude sinusoidal movement experiments, whereas in the present study large amplitude movements, simulated as a large number of steps accumulating over time, are investigated. Furthermore, the ED model is purely phenomenological as is the Hill model, but the departure point is different.

The difference of the ED model compared to the MH model is the substitution of (4–7) by (8), which describes the active dynamic behaviour of the contractile machinery. Both models contain the same length–tension function for CE, PEE and SEE (Eqs. 1–3; see also Fig. 1).

As little information is available in the literature on parameter values, the following approach was used. Time constants c, b and a were taken from Kawai and Brandt (1980), as determined on rabbit psoas muscle. A combination of parameters D, C, B and A were subsequently determined by fitting a simulation of a single experimental shortening contraction. These parameters were normalised for muscle characteristics (lo_{ce} and F_o). The ξ parameter was introduced to acknowledge the difference between eccentric and concentric behaviour, and determined by simulation of a single eccentric contraction while using all other previously determined parameters. This set of parameter values was used for all subsequent simulations (Table 2).

3 Experiments

Five young adult male Wistar rats (body mass 312 ± 9 g) were anaesthetised with pentobarbitone (initial dose 10 mg/100 g body mass i.p.). The medial head of the gastrocnemius (for description see Table 3) was freed from its surrounding tissues leaving the muscle origin and blood supply intact. The calcaneus was cut, leaving a part of bony tissue attached to the Achilles tendon, which was used to anchor the fixation of the tendon to a steel wire hook. The steel wire was connected to a strain gauge force transducer. All measurements were performed at an ambient temperature of 30 ± 0.5 °C using a muscle puller. The muscle was excited by supramaximal stimulation of the distal end of the severed nerve (square pulses; 0.5 ms duration, 3 mA, 100 Hz).

Table 3. Muscle morphometric and performance descriptors (n = 5). All values (mean ± SD) are determined by means of least-square fitting procedures for each individual muscle. Normalised values on basis of Fo and lo_{ce} if known, otherwise fibre length

Parameter		Mean ± SD
Maximum isometric force (N)		11.5 ± 0.7
$lo_{fibre} \cdot lo_{ce}$	(mm)	14.2 ± 1.1
$lo_{tendon} \cdot lo_{see}$	(mm)	30.8 ± 0.7

The stiffness of the SEE of the muscle-tendon unit was determined by performing 210-Hz vibrations during contractions at forces varying from less than 1 N ($<10\%$ F_o) up to F_o (Ettema and Huijing 1994). The different force levels were obtained by performing the same experiment at different muscle lengths. For each contraction the isometric force was measured before onset of the 210-Hz vibrations. These data, corrected for series elastic elongation, yielded the length–force characteristics of the CE (Ettema 1996). The force–stiffness data and length–force data were fitted according to (1) and (3), respectively. From the same experiments, passive force levels were obtained prior to activation, with data fitted according to (2).

CE force–velocity characteristics were determined by applying isokinetic contractions with speeds varying from −60 mm s^{-1} to +8 mm s^{-1} (Ettema and Huijing 1988; Ettema 1996). The force levels during the middle of the shortening period (i.e. at lo) were fitted against the velocities using (4).

All results on the fundamental element properties are shown in Fig. 1D.

4 Results

4.1 Main experiments

Some comparisons of models and experimental data in isokinetic force–velocity contractions are shown in Fig. 2. The models show an initial force rise at the onset of stimulation that is faster than the experimental rise. As all models show similar behaviour, it is most likely to be due to a rise in Q that is modelled too steeply [$Q(t)$ is the only property not based on rat gastrocnemius experiments]. During the isokinetic period the MH and ED models describe the force transients better than the H model.

4.1.1 Force during shortening

Force levels were compared statistically at the point where the muscle reached optimum length during the isokinetic period and just prior to relaxation, i.e. during the isometric after-phase. In all cases the HM and ED models better predict the force levels during the isometric after-phase compared to the H model. The results regarding prediction of force levels are shown in Fig. 3. The statistical comparison was done by means of a two-way analysis of variance (ANOVA) with model or

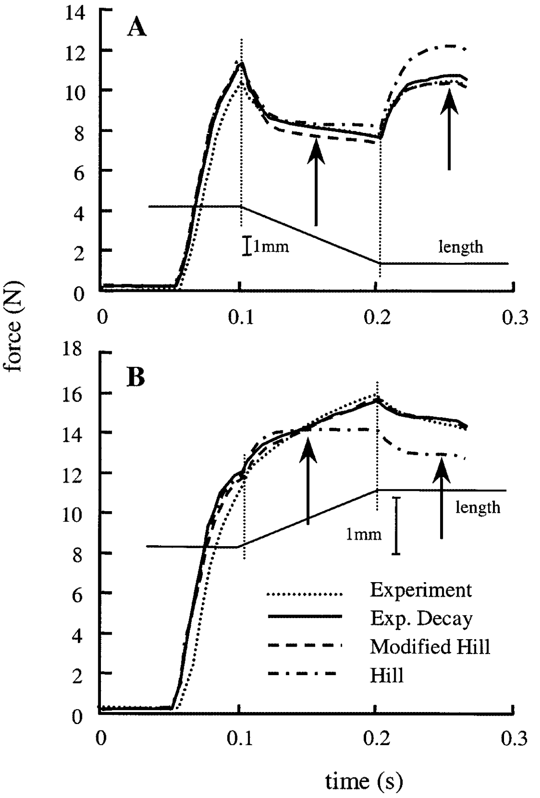

Fig. 2. Experimental and simulated force traces for two isokinetic contractions at optimum length (**A** −27 mm s^{-1}; **B** +8 mm s^{-1}). Stimulation starts at 0.05 s (just prior to initial force rise). The *vertical arrows* indicate time points at which force levels were compared (mid-isokinetic and isometric after-period). Just after the isometric force measurement (0.25 s) stimulation was ended. Length traces are illustrative only

experimental data and velocity as parameters. A Tukey post-hoc test was used to localise effects. Figure 3A shows the experimental and simulated force–velocity curves. Isometric and isokinetic force levels were separately tested as two different outcomes. The H model predicts the force–velocity best, with no significant difference between model and experimental results (average force difference < 0.01 N, $P = 0.999$), whereas both MH and ED models show a significant prediction error (0.41 N, $P < 0.001$ and 0.52 N, $P < 0.001$, respectively). The good similarity between experiment and the H model simulation (which has no history) is not surprising since the experimental force–velocity curve was used in the simulation model; in principle, the H model simulation should predict the fitted force–velocity curve (Eq. 4). More important is that the MH and ED model simulations show only small deviations from the experimental force–velocity curve. In other words, the history effect in the MH model is small, and the force–velocity characteristics derived from isokinetic contractions are also predicted well by the ED model. It should be noted that the experimental force–velocity data that are used in the MH model are slightly contaminated by history effects. That is, at the point of measurement in the middle of the isokinetic period, the CE has already undergone considerable length change, inducing a history effect. Furthermore, the interaction between velocity and model was significant ($P < 0.01$), indicating that the different models predict with changing accuracy along the measured velocity range. Yet these effects remain small in the absolute sense (Fig. 3A).

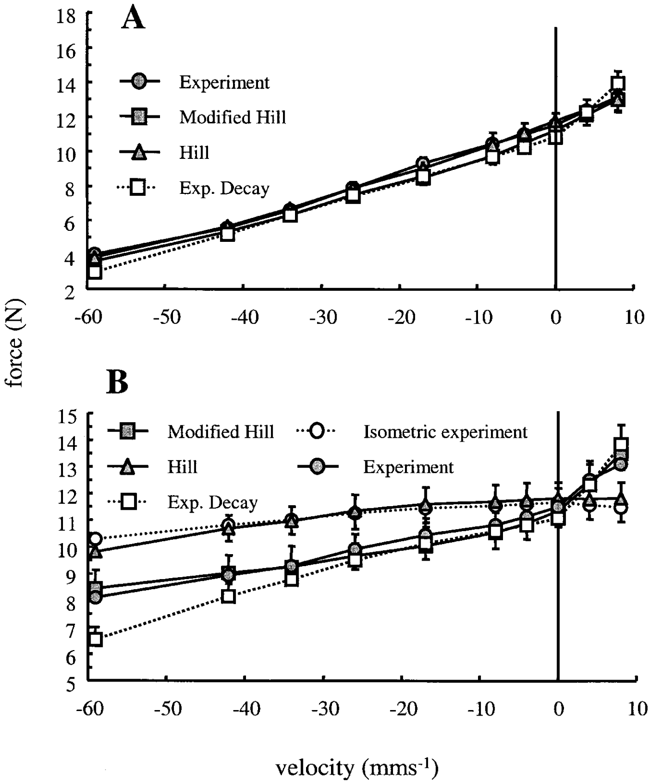

Fig. 3. Mean values of experimental and simulated force levels during isokinetic length change (**A**) and during the isometric after-period (**B**), as a function of the isokinetic shortening velocity of the contraction. The simulations were performed for all individual muscles based on their individual characteristics (Eqs. 1–4). *Vertical bars* indicate SD for experiments and simulations ($n = 5$)

4.1.2 Force during the isometric period after shortening

In Fig. 3B, two types of experimental data are plotted. First, the measured forces during isometric after-periods of the isokinetic contractions are shown. Secondly, the purely isometric forces are shown, which were predicted on the basis of the experimental isometric length–tension curve and the length of the muscle in the isometric after-period (which was slightly different for different velocities). The differences between the two sets of experimental data indicate history effects, i.e. shortening-induced force depression and stretch-induced enhancement. These experimental data are compared with the model predictions. The H model simulation predicts the purely isometric (experimental) forces, and are significantly different from the experimental forced during the isometric after period (ANOVA, Tukey post-hoc test, average error −0.76 N, $P < 0.001$). The MH and ED models predict the experimental results quite well. Except for the highest shortening velocity in the ED model, the error is 5% or less (average error 0.07 N, $P = 0.467$ and 0.02 N, $P = 0.976$, respectively).

Furthermore, a significant interaction effect ($P < 0.01$) also indicates different behaviour of the models and experimental data over the velocity range, which is due to the behaviour of the H and ED models. From Fig. 3B it is clear that the ED model overestimates the shortening-induced force decay at an increasing rate with shortening velocities beyond 30 mm s^{-1}. The difference between the ED model and experimental results becomes statistically not significant when the 60-mm s^{-1} data are excluded. The velocity dependence in the H model (which does not predict any history effect) is obvious, as any (experimental) history effect increases with the amplitude of shortening, and thus velocity in this set-up.

4.2 Additional experiments

4.2.1 Comparing contractions with equal length changes

In the main experiments, the influence of shortening velocity was examined by changing the movement amplitude while maintaining a similar movement time. To obtain more insight into possible interactions of the time, amplitude and velocity of movement, extra simulations were performed on shortening contractions of equal movement distance but with different movement time and velocity (Fig. 4). It is known that force depression in fast but short-lasting movements is less than in slow but longer movements of the same amplitude (Meijer et al. 1998). This aspect is incorporated in the MH model (Meijer et al. 1998) and these simulations therefore demonstrate this feature. The ED model predicts the opposite finding and thus does not predict this more detailed aspect of force depression.

The third experimental paradigm, that of comparing movements of the same velocity but with different amplitudes and durations, was not investigated in such detail, as the results are obvious (i.e. the history effect will increase with amplitude).

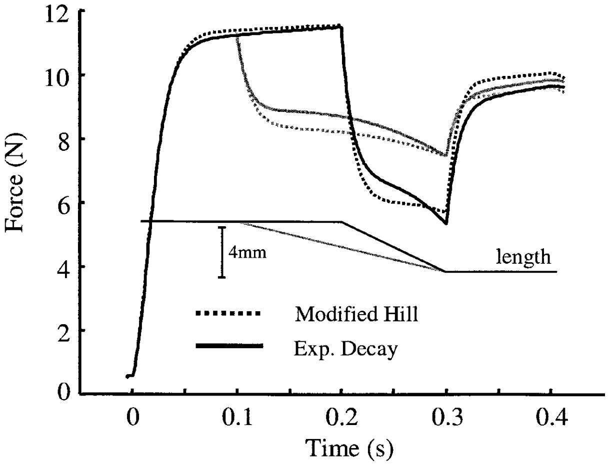

Fig. 4. Simulations of two isokinetic shortening contractions using the MH and ED models. Shortening distance is 4 mm in both contractions; shortening duration and velocity are 0.1 and 0.2 s, and 40 mm s^{-1} and 20 mm s^{-1}, respectively. Note that the relative force depression for the two contractions are opposite in the MH and ED models, with the MH model outcome fitting experimental results (Meijer et al. 1998)

4.2.2 Long-lasting contractions

The main experiments were set up to specifically study transient characteristics during relatively brief contractions (less than 300 ms). However, it is argued in the literature that force potentiation and depression effects are long lasting, and maybe even permanent during long-lasting contractions (Morgan 1990; Herzog and Leonard 1996; Herzog 1998b). Thus, it was of interest to study the force transients over a longer period than was done in the experimental study, while using the current parameters settings including the permanent component D of the ED model (see Eq. 8), that show good performance in short duration contractions (Fig. 5). In Fig. 5A, simulation results are shown of a shortening contraction with a long-lasting isometric after-period. Where the H model reaches isometric force level within 50 ms, the MH model still shows some force depression at the end of the contraction, even though only transient (and not permanent characteristics) were implemented in this model. The initial transient behaviour in the ED model transforms into a permanent depression that is directly dependent on the D parameter value. Figure 5B shows experimental and normalised simulation results for shortening and lengthening contractions that were

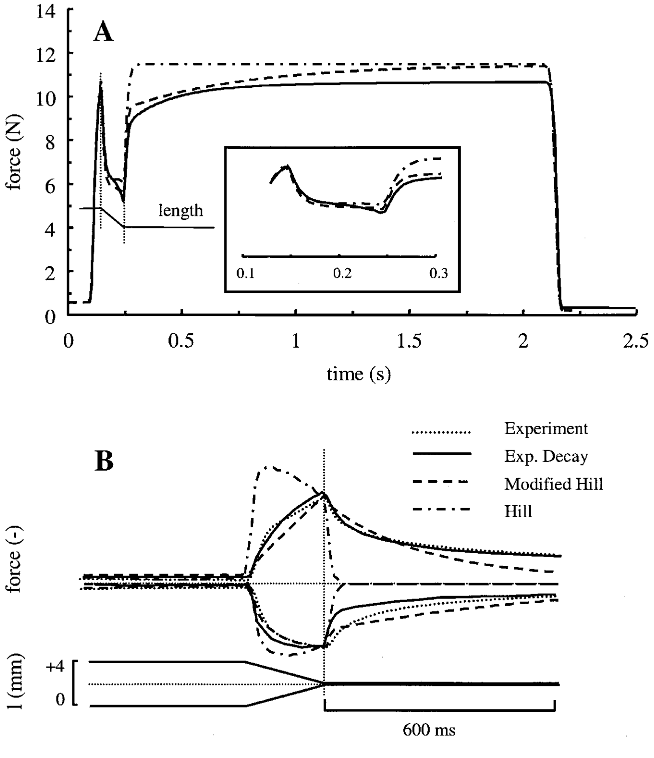

Fig. 5. **A** Simulation force traces of long-lasting contractions with an isokinetic shortening of −35 mm s^{-1} (movement indicated), to show the force transient during a long-lasting isometric after-period. The *inset* shows the shortening period and first 50 ms of isometric contraction in more detail. **B** Normalised force traces (experimental and simulations) of a shortening and stretch contraction with a 600-ms isometric after-period. The normalisation extracts the time transients of simulations compared to experimental traces

performed on one muscle, where the isometric after-period lasted more than 0.6 s. The purpose of this particular comparison was to study force–time dependence. Therefore, the simulation force levels were adjusted to experimental force levels at the end of the isokinetic period. Where the H model shows short-lasting force transients during the isometric phase (about 50 ms), the other models show force depression (after shortening) and force enhancement (after stretching) during the entire isometric after-period. However, with exception of the ED model after stretching, the models clearly do not predict well the entire force trace during depression and enhancement.

5 Discussion

The present study examined three models that predict the effects of muscle length changes during subsequent isometric contraction: a classic Hill model (as a reference), a modified Hill model that included a 'memory function', and a third phenomenological model with its origin in the mechano-chemical description of the cross-bridge cycle (Kawai and Brandt 1980). Their behaviours were compared with experimental data. The latter two models describe major aspects of force generation during and after slow-ramp movements reasonably well for relatively short time periods (the predictive power depending on the model and type of contraction). However, the long-term behaviour was only partially described by the models. Possible reasons for these results will be discussed and some hypotheses concerning the mechanism of contraction will be formulated.

5.1 Force–velocity characteristics

The ED model predicts force transients equally well as the MH model, including the force–velocity characteristics during isokinetic movements. This finding emphasises the phenomenological property of the force–velocity curve. Unlike the length–tension curve that is explained by structural models, the force–velocity curve can be considered as one of the many output characteristics of an underlying contraction principle. Within the Hill paradigm, contraction history is considered an adjustment of the fundamental length–force and force–velocity properties of muscle (e.g. Herzog and Leonard 1996, 1997; Meijer et al. 1998; Huijing 1998). Yet, in the ED model, contraction history and force–velocity characteristics are two behavioural manifestations of a single underlying fundamental property of muscle (possibly the mechano-chemistry of the cross-bridge cycle). This property is described as an interaction between length change, time and force change (Eq. 8), and thus implicitly entails a (unspecified) relationship between force and velocity (length change over time) for any set of contractions. One of these relationships is the classic force–velocity curve, determined by a set of contractions at different movement velocities (i.e. different length changes over the same time period or a constant length change over different time periods). We therefore argue that the force–velocity curve should be considered a behavioural outcome of another underlying property since, unlike the length–tension curve, the force–velocity curve has no evident structural basis. Thus, at least a part of movement-induced force enhancement and depression should not be considered as alterations to the length–tension or force–velocity curve (e.g. Huijing 1998), but rather, together with the classic force–velocity characteristic, as a single time-dependent response to length change. In mechanical terms, the finding that a muscle works as a low-pass filter with a phase delay does not indicate that the contraction mechanism is based on a biological version of a spring-dashpot system (Hill model), a seemingly obvious conclusion, but one that is often ignored in the literature.

By approaching muscle contraction from a mechano-chemical perspective, the short-term force response can be predicted better than when using the Hill-type approach, which requires large phenomenological modifications (e.g. MH model: Meijer et al. 1998). Modifications of the cross-bridge theory (Huxley 1957), based on structural information, have been proposed to explain long-lasting shortening-induced force depression effects (Herzog and Leonard 1997; Herzog 1998b). Yet, the current study suggests that a large component of the (slow) transient effects can be described without these modifications, by using a different phenomenological description of the dynamics (see also Sect. 5.2).

5.2 Short duration vs long duration effects

The MH and ED models show a creep in all of the movement-induced force transients towards the isometric force level predicted on the basis of the length–tension characteristics. Although both models predict the transient well for about 50–200 ms, a too-high rate of force change is seen afterwards (Fig. 5). The predictive power of the ED model could probably be improved by altering the parameters presented in Table 1. However, that would be merely a fitting procedure of the current experimental results. In this respect, it should once more be noted that the parameter set used was based partly on a curve fitting procedure in a single experiment. Furthermore, the time constants are based on the study by Kawai and Brandt (1980) that considered only short-amplitude vibrations. Short-amplitude contractile behaviour (with little or no myofilament sliding) is dissimilar from large-amplitude movement behaviour (e.g. Ettema 1996). Furthermore, Kawai and Brandt (1980) presented a model in the Laplace domain which responded to a step input as the sum of three exponentials. The ED model, on the other hand, applies such exponentials to ramp movements as an accumulation of many small and rather slow steps. Thus, it is not evident how valid the current parameter values actually are. Still, the results indicate the potential of the ED model in the prediction of a movement-induced force response. New, more fundamental experiments are required to estimate the constants independently.

The ED model will predict any permanent force deviation (depression or enhancement), depending on the *D* value but independent of the other parameter values. Note that the current version of the MH model only contains transient history effects, and therefore cannot predict permanent force deviations (the MH model could be improved quite easily on this point). Herzog and Leonard (1997) have demonstrated a long-lasting shortening-induced force depression in cat soleus. Their results indicate that apart from a slow transient force depression, there is also a permanent depression component. Morgan (1990) describes similar behaviour for stretch-induced enhancement. Herzog and Leonard (1997) and Morgan (1990) propose plausible structural changes of sarcomeres as the cause of history effects: the 'popping sarcomere' model (Morgan 1990) and the 'work-performed' model (Herzog and Leonard 1997; Herzog 1998b). The ED model proposes that contraction history, as defined currently in the literature, may have two distinct causes. Firstly, the fundamental characteristics of cross-bridges predict dynamic time-dependent behaviour that logically deviates strongly from the classic time-independent three-dimensional length-force-velocity surface description of muscle. This behaviour is described by the three time-dependent components [Ce^{ct}, Be^{bt} and Ae^{at} in Eq. (8)]. Secondly, movement-induced structural changes of the myofilaments and cross-bridges may induce permanent time-independent deviations in force production from this length-force-velocity surface (e.g. Morgan 1990; Herzog and Leonard 1997; Herzog 1998b), which is described by parameter *D* in the model. The fact that the ED model fails to predict a lesser force depression in fast but short-lasting shortening contractions (Fig. 4) may be an indication that the permanent component is more complex than how it is described here (i.e. linearly related to length change).

In the ED model, the effects of muscle length on the magnitude of history effects were not implemented. Such interactions, however, have clearly been demonstrated (see Sect. 2). This may partly explain the relatively poor prediction of the ED model in the additional experiment (Fig. 5B) that was performed at 2 mm higher than optimum length. It is obvious that such interactions should be implemented in future models. Models as proposed by Herzog and Leonard (1997) and Herzog (1998b), who explain force depression by the stress on the actin filaments and related deformation of unattached cross-bridges that enter the overlap zone, may give the opportunity to do so.

5.3 Concluding remarks

In integrated daily-life movement, skeletal muscle contractions are often dynamic and of short duration. Thus, muscle models as sub-parts of an entire system should perform particularly well for such contractions. Furthermore, modelling integrated musculoskeletal behaviour requires relatively simple models of subsystems (e.g. muscle) because of the increasing complexity at the integrated level (e.g. Bobbert 1991). The ED modelling approach of muscle contraction conforms to both requirements and thus may prove very useful in modelling integrated musculoskeletal action. The approach applied here for determining parameter values in the ED model seems reasonable and the values are plausible, yet the underlying logic of using data based on step responses for ramp movements is rather weak. Thus, future studies on the parameter values in the ED model that apply to the current contraction dynamics must verify these conclusions.

References

Beek PJ (1991) Modelling complexity: a complicated business. In: Jacobs R, Rikkert WEI (eds) Movement Control. An Interdisciplinary Forum. VU University Press, Amsterdam, pp 91–96

Bobbert MF (1991) Required performance. In: Jacobs R, Rikkert WEI (eds) Movement Control. An Interdisciplinary Forum. VU University Press, Amsterdam, pp 85–89

Calancie B, Stein RB (1987) Measurement of rate constants for the contractile cycle of intact mammalian muscle fibers. Biophys J 51: 149–159

de Ruiter CJ, De Haan A, Jones DA, Sargeant AJ (1998) Shortening-induced force depression in human adductor pollicis muscle. J Physiol (Lond) 507: 583–591

Edman KAP (1975) Mechanical deactivation induced by active shortening in isolated muscle fibres of the frog. J Physiol (Lond) 246: 255–275

Edman KAP (1980) Depression of mechanical performance by active shortening during twitch and tetanus of vertebrate muscle fibres. Acta Physiol Scand 109: 15–26

Edman KAP, Elzinga G, Noble MIM (1978) Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. J Physiol (Lond) 281: 139–155

Ettema GJC (1996) Contractile behaviour in skeletal muscle-tendon unit during small amplitude sine wave perturbations. J Biomech 29: 1147–1155

Ettema GJC, Huijing PA (1988) Isokinetic and isotonic force-velocity characteristics of rat EDL at muscle optimum length. In: de Groot G, Hollander AP, Huijing PA, van Ingen Schenau, GJ (eds) Biomechanics XI-A, International Series on Biomechanics 7-A. Free University Press, Amsterdam, pp 58–62

Ettema GJC, Huijing PA (1994) Frequency response of rat gastrocnemius medialis in small amplitude vibrations. J Biomech 27: 1015–1022

Ettema GJC, Huijing PA, van Ingen Schenau GJ, de Haan A (1990b) Effects of prestretch at the onset of stimulation on mechanical work output of rat medial gastrocnemius muscle-tendon complex. J Exp Biol 152: 333–351

Ettema GJC, van Soest AJ, Huijing PA (1990a) The role of series elastic structures in prestretch induced work enhancement during isotonic and isokinetic contractions. J Exp Biol 154: 121–136

Ettema GJC, Huijing PA, de Haan A (1992) The potentiating effect of prestretch on the contractile performance of rat gastrocnemius medialis muscle during subsequent shortening and isometric contractions. J Exp Biol 165: 121–136

Granzier HLM, Pollack GH (1989) Effect of active pre-shortening on isometric and isotonic performance of single frog muscle fibres. J Physiol (Lond) 415: 299–327

Hatze H (1981) Myocybernetic control models of skeletal muscle. University of South Africa, Pretoria

Herzog W (1998a) Muscle modelling (Editorial). J Electromyogr Kinesiol 8: 59–60

Herzog W (1998b) History dependence of force production in skeletal muscle: a proposal for mechanics. J Electromyogr Kinesiol 8: 111–117

Herzog W, Leonard TR (1996) History-dependence of muscular force: shortening contractions. In: Hoffer JA, Chapman A, Eng JJ, Hodgson A, Milner TE, Sanderson D (eds) Proceedings of the 9th Biennial Conference and Symposia of the Canadian Society for Biomechanics. Conference Organising Committee, Burnaby, British Columbia, pp 256–257

Herzog W, Leonard TR (1997) Depression of cat soleus-forces following isokinetic shortening. J Biomech 30: 865–872

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc Lond B Biol Sci 126: 136–195

Huxley AF (1957) Muscle structure and theories of contraction. Prog Biophys Chem 7: 255–318

Huijing PA (1995) Parameter interdependence and success of skeletal muscle modelling. Hum Mov Sci 14: 443–486

Huijing PA (1998) Muscle, the motor of movement: properties in function, experiment and modelling. J Electromyogr Kinesiol 8: 61–77

Kawai M (1982) Correlation between exponential processes and cross-bridge kinetics. In: Twarog BM, Levine RJC, Dewey MM (eds) Basic Biology of Muscle: a Comparative Approach. Raven Press, New York, pp 109–130

Kawai M, Brandt PW (1980) Sinusoidal analysis: a high resolution method for correlating biochemical reactions with physiological processes in activated skeletal muscles of rabbit, frog and crayfish. J Muscle Res Cell Motil 1: 279–303

Lee H-D, Suter E, Herzog W (1999) Force depression in human quadriceps femoris following voluntary shortening contractions. J Appl Physiol 87: 1651–1655

Meijer K, Grootenboer HJ, Koopman HJFM, Huijing PA (1997) Fully isometric length-force curves of rat muscle differ from those during and after concentric contractions. J Appl Biomech 13: 164–181

Meijer K, Grootenboer HJ, Koopman HJFM, van der Linden BJJJ, Huijing PA (1998) A Hill type model of rat medial gastrocnemius muscle that accounts for shortening history effects. J Biomech 31: 555–563

Morgan DL (1990) New insights into the behavior of muscle during active lengthening. Biophys J 57: 209–221

Otten E (1991) Modelling movement control. In: Jacobs R, Rikkert WEI (eds) Movement Control. An Interdisciplinary Forum. VU University Press, Amsterdam, pp 69–84

van Ingen Schenau GJ, Bobbert MF, Ettema GJ, de Graaf JB, Huijing PA (1988) A simulation of rat EDL force output based on intrinsic muscle properties. J Biomech 21: 815–824

van Ingen Schenau GJ, van Soest AJ, Gabreëls FJM, Horstink MWIM (1995) The control of multi-joint movements relies on detailed internal representations. Hum Mov Sci 14: 511–538

van Soest AJ, Bobbert MF (1993) The contribution of muscle properties in the control of explosive movements. Biol Cybern 69: 195–204

Walshe AD, Wilson GJ, Ettema GJC (1998) Stretch shorten cycle as compared to isometric preload: contributions to enhanced muscular performance. J Appl Physiol 84: 97–106

Winters JM (1995) How detailed should muscle models be to understand multi-joint movement coordination? Hum Mov Sci 14: 401–442

Winters JM, Woo SL-Y (1990) Multiple muscle systems: biomechanics and movement organization. Springer, Berlin Heidelberg New York

Zahalak GI (1990) Modeling muscle mechanics (and energetics). In: Winters JM, Woo SL-Y (eds) Multiple Muscle Systems: Biomechanics and Movement Organization. Springer, Berlin Heidelberg New York, pp 1–23