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A SIMULATION OF RAT EDL FORCE OUTPUT BASED ON INTRINSIC MUSCLE PROPERTIES

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Abstract—Force-velocity and force-length relations were obtained for the edl of four Wistar rats in order to characterise the contractile properties (CE) of these muscle-tendon complexes. Compliances of the undamped part of the series components (SE) were measured in quick length decreases. Force-extension relations of SEs were obtained by integration of compliance to force.

A muscle model consisting of CE, SE and a visco-elastic element was used to simulate the force output of the muscle tendon complex in response to a changing muscle length l_{OI} as input. This simulated force was compared with the experimental force of the same muscle measured in response to the same l_{OI} as input. Tetanic contractions were used in all experiments. The results show that this muscle model can predict the experimental force within a mean maximal error not larger than approximately 14% of the force amplitude. However the comparison of simulated force with experimental force and a few additional experiments show that the muscles do not have a unique instantaneous force-velocity characteristic.

As shown by several other studies, force seems to be influenced by many other variables (time, history etc.) than CE length and velocity.

INTRODUCTION

In biomechanical research on limb dynamics during complex movements, muscle models are used to simulate the macroscopic behavior of skeletal muscle.

In modelling a skeletal muscle-tendon complex, two approaches can be discerned in the literature:

(a) Hill-type models based on two or three elements as proposed by A. V. Hill (1938)

(b) Huxley-type models based on cross bridge kinetics as introduced by A. F. Huxley (1957).

In the simulation of muscle behaviour during complex movements, most biomechanists use Hill-type models; a choice which is most likely based on the attractive simplicity of these models (Zahalak, 1981). Basically the Hill-type models contain an active contractile component CE, a passive elastic component SE in series with the CE and an elastic element PE in parallel to SE, or to CE and SE (e.g. Hill, 1970; Hof *et al.*, 1983; Hatze, 1977, 1978, 1981a; Zajac *et al.*, 1984; Bobbert *et al.*, 1986a, b; Davy and Audu, 1987). It is generally assumed that the damping component of the SE is negligible (see Hatze, 1977 for references) while the influence of PE is low in contractions covering muscle lengths around or lower than the muscle optimal length l_0 (Jewell and Wilkie, 1958; Woittiez *et al.*, 1987). This means that for most *in vivo* situations the behavior of muscle-tendon complexes is described by the combination of the CE and the SE.

The two major functional properties of the CE in a fully activated muscle are assumed to be its normalised force-length [$L(x)$] and force-velocity [$F(\dot{x})$] charac-

teristics. Given the length x and contraction velocity \dot{x} of the CE, the fraction F/F_0 of the maximal isometric force F_0 is said to be uniquely determined by $L(x)$ and $F(\dot{x})$. In modelling non maximal activation levels, F_0 is influenced by transfer functions which describe the response of F_0 to nerve impulses (Hatze, 1978) or the emg to F_0 conversion (Hof and van den Berg, 1981).

Many authors, however, have pointed at shortcomings of the Hill-type models; in particular in contractions which contain an eccentric phase (e.g. Abbot and Aubert, 1952; Jewell and Wilkie, 1958; Cavagna *et al.*, 1968; Edman *et al.*, 1978; Atteveld and Crowe, 1980; Zahalak, 1981). Since the force-length dependency seems to be easily explained on the basis of filamentary overlap (Gordon *et al.*, 1966; Rome *et al.*, 1985), the various anomalies seem to provide arguments against the existence of one unique and instantaneous relation between force and velocity (Jewell and Wilkie, 1958; Zahalak, 1986; Huxley, 1985). Force-velocity relations are derived by fitting equations to points obtained in separate contractions. Direct measurements of CE instantaneous force-velocity characteristics in one contraction with different velocities is difficult since the length and the shortening velocity of the series elastic component can not directly be measured in such contractions. For this reason series of isotonic or isokinetic contractions are used to construct these relations for a fixed muscle length.

In a previous study (Ingen Schenau *et al.*, 1985) it was shown that the instantaneous torque-angular velocity in plantar flexion during jumping was completely different from the hyperbolic relation reported for force and velocity in isolated muscles or for torque and angular velocity constructed on the basis of

isokinetic plantar flexions. For jumping, combinations of torque and angular velocity were found which represent a power output which is six times larger than the maximal power output which can be achieved by isokinetic plantar flexions. In a later study Bobbert *et al.* (1986a, b) applied a model of the triceps surae consisting of contractile and series elastic elements with characteristics estimated on the basis of the architecture of these muscles. Using the contraction velocities V_{OI} (the velocity difference between origin and insertion of both the gastrocnemius and soleus) as input, the simulation could adequately explain the discrepancies reported by Ingen Schenau *et al.* (1985).

Remaining questions of course concern the reliability of the estimations of the force-length and force-velocity characteristics of the CEs as well as the assumed compliance of the series elastic components.

Surprisingly few studies are performed to test this reliability of the simulated behavior of skeletal muscles based on Hill-type models. In a simulation (based on numerical integration) of force development under different (concentric) conditions at fixed origin-insertion distance l_{OI} , Jewell and Wilkie (1958) already found a significant difference between their simulated curves based on (measured) functional properties and the actual force time curves measured on the same muscle.

The purpose of the present study was to extend Jewell and Wilkie's type of simulation to contractions which involve eccentric and concentric phases in response to a varying l_{OI} . Since the immediate cause for these experiments was actuated by the above mentioned study to the behavior of human calf muscles, a muscle with a relatively long tendon was selected for the experiments.

METHOD

Material

The muscle selected for the experiments was the extensor digitorum longus (edl) of adult Wistar rat which has a mean fibre length of approximately 25% of total muscle length (Woittiez *et al.*, 1987). Five animals were anaesthetised by means of Nebutal (0.12 mg g^{-1}). The distal end of the muscle and tendon was dissected free from surrounding tissue. The proximal end was fixed by securing the femur. The insertion was connected to a force transducer by means of a metal clamp to which the tendon was tightly glued. Relative humidity and ambient temperature were kept at $95 \pm 5\%$ and $24 \pm 1^\circ\text{C}$ respectively. Tetani were applied by stimulating the distal end of the severed nerve (100 Hz). Muscle optimum length (l_o) was determined from the force-length curve. Periods of muscle activity were separated by 2 min intervals rest at a muscle length lower than l_o where the muscle was allowed to recover. To enable the muscle to adjust to each desired initial length, two twitches were evoked prior to each tetanus.

Ergometer

The muscle ergometer which has been described previously (Woittiez *et al.*, 1987) consists basically of a linear motor-servo control system with options for force and length control. In the present experiments the length control mode was used. The compliance of the force measurement system is $20 \mu\text{m N}^{-1}$.

SE-compliance

The compliance of the SE of the edl muscle-tendon complex was determined by the force response to small fast length decreases of 0.25 mm within 4 ms at different force levels. These force levels were obtained during tetanic contractions at different muscle lengths. Given an average muscle length of $l_o = 4.78 \text{ cm}$ the length steps are about 0.5% l_o which is considerably smaller than the maximal extension range of the SE (Morgan *et al.*, 1978) and the velocity of the step is approximately $1.31 l_o \text{ s}^{-1}$. Though this velocity is slightly lower than the maximal velocity of shortening of the edl (Woittiez *et al.*, 1987; Ranatunga, 1984) it was shown before that the compliance measurement is not affected by the velocity of the step in the velocity range of $0.9\text{--}1.3 l_o \text{ s}^{-1}$ (Bobbert *et al.*, 1986c). Nevertheless it can not be excluded that this limitation of maximal step velocity of the ergometer might lead to a slight overestimation of the SE compliance. From the compliance-force relation, the force-extension relation of the SE was calculated. Though many different mathematical functions are proposed in the literature (Hof *et al.*, 1983; Hatze, 1978; Proske and Morgan, 1987), it was shown before that the overall force-extension relation of the SE can fairly well be approximated by $F = k_s \Delta l^2$ where k_s is a constant and Δl is the extension of the SE (Ingen Schenau, 1984). It should be noted that this approximation will only be reliable in a muscle-tendon complex of which SE compliance is mainly determined by passive tendinous structures which lie in series with the elastic components of the cross bridges. Though it is well known that part of SE of a muscle-tendon complex is located in the muscle fibres and more in particular in the cross bridges (Huxley, 1974; Bressler and Clinch, 1975; Ford *et al.*, 1981), it is also known that the influence of this part of the SE in the overall force-extension relation of the SE is small. At maximal isometric force (F_o), the extension of the cross bridge compliance is reported to be in the order of magnitude of 4–12 nm per half sarcomere (Huxley, 1974; Bressler and Clinch, 1975; Cecchi *et al.*, 1982; Ford *et al.*, 1981). This accounts for 0.5–1.5% of fibre optimal length and thus for 0.1–0.4% of l_o of the total muscle-tendon complex of rat edl if relative lengths of fibres and tendon (Woittiez *et al.*, 1987) are taken into account. Total extension of the SE at F_o for muscles with relatively long tendons however is reported to be in the order of magnitude of 2–5% of l_o (Bobbert *et al.*, 1986c; Walmsley and Proske, 1981; Morgan *et al.*, 1978; Morgan, 1977). This means that the major part of the SE is located in passive structures

in series with the fibres. This result can also be deduced from measurements of Morgan *et al.* (1978) who showed that in gastrocnemius muscle of Kangaroos extension in the tendon at F_o is eight times larger than the SE extension in muscle fibres. This means that the SE force extension curve follows to a large extent the behaviour of tendinous structures which are shown to have an increasing stiffness as force increases (Stöke, 1950; Abrahams, 1967; Arnold, 1974). This relationship is satisfactorily approximated by a quadratic equation (Ingen Schenau, 1984).

If $F = k_s \Delta l^2$ is used as a starting point, the compliance data of the present measurements should follow the function

$$\frac{\Delta l}{\Delta F} = \frac{1}{2\sqrt{k_s F}} \quad (1)$$

where ΔF is the response of F on the length step Δl . With this equation the compliance data were fitted to solve the k_s values of the muscles. Since quick release experiments do not account for an eventual damped part of the SE in series with the undamped part, a visco-elastic element was also used in the simulations described below.

CE force-length relation

The force-length relation was determined by measuring the force during tetanic contractions at different muscle lengths around l_o . In steps of 1 mm the force was measured from $l_o - 6$ mm to $l_o + 3$ mm. To calculate the force-length relation of the contractile element CE, SE extension at each muscle length was calculated from force and SE force extension curve and subtracted from the total muscle length (Abbot and Wilkie, 1953). This reconstructed CE force-length relation was fitted by means of a second order function of the form

$$F = a_0 + a_1(x - x_o) + a_2(x - x_o)^2$$

where a_0 , a_1 and a_2 are constants and x and x_o represent the length and optimal length of the CE respectively. Fitting was performed on five-six data points around optimal length only since the movement which was to be simulated took place in a small range around l_o (see below).

As can be deduced from the data provided by Woittiez *et al.* (1987) for rat edl and by Jewell and Wilkie (1958) for frog sartorius, the influence of the PEC can be neglected in this length range.

Force-velocity relation

Tetanic force was measured at l_o during isokinetic contractions ranging from -7 mm s⁻¹ to $+50$ mm s⁻¹. The initial and final muscle length as well as the onset of stimulation was controlled by a microprocessor system in such a way that l_o was always passed at the 20th stimulation pulse. This was done to standardise the time history of the contractions at all velocities. Though a number of other functions were

used to fit the datapoints (see discussion section), Hill's hyperbolic function was chosen for the concentric area in order to be able to simulate a Hill-type model as used in most referred studies. Moreover, in Hill's function F_o lies on the fitted curve which makes it more easy to create a continuous curve at $v = 0$. A second order function $v = A_0 + A_1 F + A_2 F^2$ (A_0 , A_1 and A_2 being constants) was fitted to F_o and the two data points in the eccentric area (0 to -6 mm s⁻¹). The latter was done since the simulations appeared to be highly sensitive to this fitting procedure (see Discussion). This procedure led to a continuous $F-v$ curve though the slope could show a discontinuity at $v = 0$. This however does not seem to contradict the underlying phenomena which cause enhancement of force in eccentric contractions and deficit of force in concentric contractions (relative to F_o) and which seem to be caused by different mechanisms (Tsuchiya and Sugi, 1986).

Simulations

In order to achieve a driving function l_{OI} for simulation of force output of the muscle, an eccentric-concentric pattern was chosen in order to simulate a more or less 'natural' movement. This input function is presented in Fig. 1. The function was obtained by filtering a function used for a continuous sequence of an isokinetic eccentric contraction immediately followed by an isokinetic concentric contraction (Fig. 1). The latter is used in many physiological experiments (e.g. Cavagna *et al.*, 1968). The filtering removed the unnatural discontinuities in the velocity pattern (Fig. 1). To study the response to fast changes of velocity, simulations were also performed with the unfiltered l_{OI} function as input. Simulated force output is compared with force output measured when the driving functions were used as input for the experimental muscle. Since only maximal stimulations were used, the simulations could only be performed in a limited eccentric-concentric range and at relatively low velocities. Previous experiments showed that beyond this range, the muscle is easily damaged during the eccentric phase of the contractions. This of course limits the predictive value of the results of this study for simulation of real life movements.

For the simulation a model was used according to Fig. 2. In series with the CE (which contained the force-length and force-velocity characteristics) and to the undamped SE, a visco-elastic element was used for additional simulations. This visco-elastic element was assumed to consist of an elastic element with a quadratic force-extension characteristic in parallel to a dashpot with a linear force-velocity dependency. In the undamped simulations this visco-elastic element was given an extremely high stiffness and viscosity. For low values of the stiffness, a new CE force-length relation had to be calculated prior to simulation on the basis of the extension of the total SE at isometric contraction. After calculation of initial coordinates

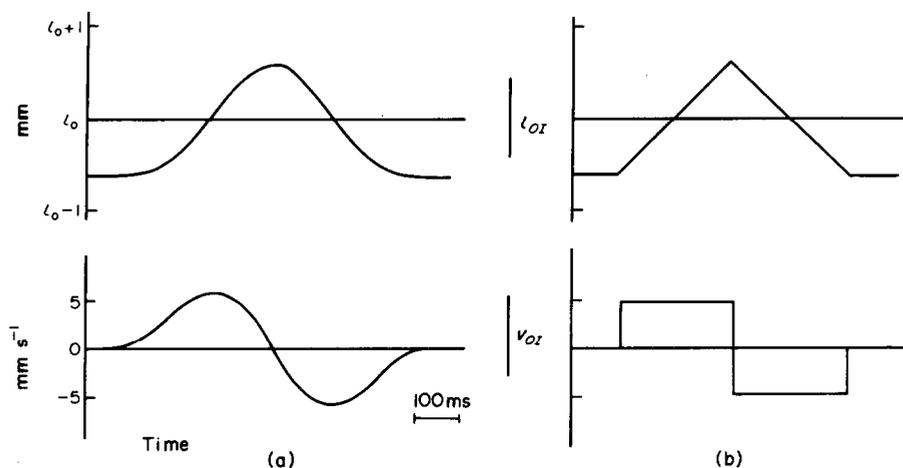


Fig. 1. The changing muscle lengths, l_{OI} which were used as input for the simulation and their derivatives v_{OI} .

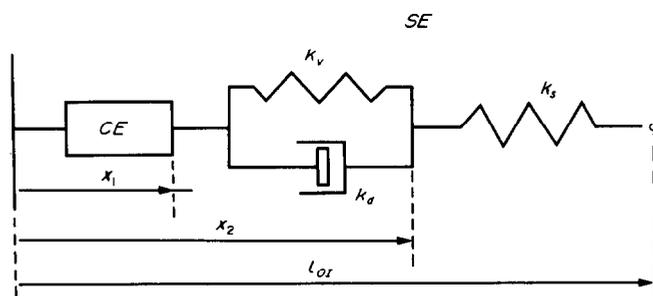


Fig. 2. The model used for the simulation. The elastic components have both a quadratic force-extension characteristic with k_v and k_s as proportionality constants. For the dashpot a linear force-velocity dependency is assumed with k_d the proportionality constant.

and force at the initial l_{OI} simulation was performed in steps of 1 ms (experimental force and length were sampled at 1000 Hz). One step in the simulation contained the consecutive calculation of the following new variables (see Fig. 2): new force F of the undamped part of SE, new normalised force of CE as a function of F and CE-length, new contraction velocity (\dot{x}_1) of the CE, new forces in both elements of the damped part of the SE, new velocity $\dot{x}_2 - \dot{x}_1$, new x_1 , new x_2 , next l_{OI} .

During the course of all experiments maximal isometric force was measured five times. If F_o showed a deviation of more than 10% from its initial value, the data were excluded. To avoid the influence of a small decrease of F_o in the course of the experiments, which was seen in all muscles, the force-length relation was

normalised to the F_o measured during the isokinetic experiments. Moreover the forces measured at the initial lengths l_{OI} were normalised to the initial force which the muscle should have on the basis of its force-length relation at this (isometric) initial value of l_{OI} .

RESULTS

The results of one of the five rats had to be excluded since the repeated measurements of F_o showed a decrease in forces during the course of the experiments of more than 10%.

Parameter values of the four remaining muscles are summarised in Table 1. The compliance-force data are

Table 1. Parameter values of the four edl muscles

Muscle number	F_o (N)	l_o (mm)	a/F_o	k_s ($N m^{-2}$)	SE-extension at F_o
1	2.10	59.5	0.12	$6.3 \cdot 10^5$	3.1%
2	1.07	43.7	0.20	$5.0 \cdot 10^5$	3.3%
3	2.37	41.3	0.31	$1.1 \cdot 10^6$	3.1%
4	2.25	46.7	0.15	$1.1 \cdot 10^6$	3.0%

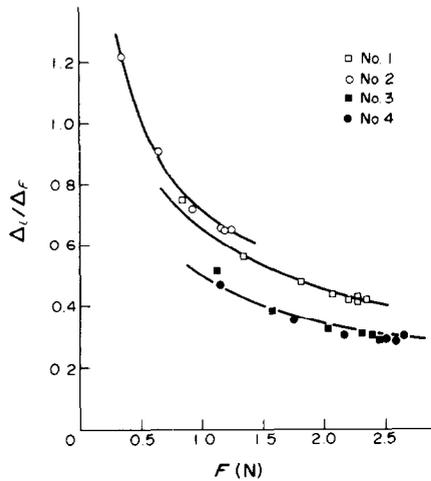


Fig. 3. Compliance as a function of muscle force for four muscles. The solid lines represent parts of equation (1) with different k_s values.

presented in Fig. 3. The data points were fitted (the solid lines in Fig. 3) by means of equation (1), two muscles (nos. 3 and 4) having the same k_s . The mean value of the constant k_s of undamped SE was $8.3 \cdot 10^5 \text{ N m}^{-2}$ (range of $5.0 \cdot 10^5$ – $1.1 \cdot 10^6$). At F_o this corresponds with an extension of 3.0–3.3% of l_o . These figures are within the range of SE extensions of 2–5% reported by others (Morgan, 1977; Morgan *et al.*, 1978; Walmsley and Proske, 1981; Bobbert *et al.*, 1986c), or which can be calculated from stiffness or compliance data (Rack, 1985; Rack and Westbury, 1984) on the basis of equation (1).

Figure 4 shows a typical example of a force–length relation. The dashed line is drawn by hand through the data points which are calculated by subtraction of the SE extension from l_{O1} at each force. The force–velocity relation of the same muscle is presented in Fig. 5. Hill's hyperbolic equation fits the data well though slight improvements may be possible when other functions are used (Hatze, 1978; Marsh and Bennet, 1986). The mean value found for the characteristic constant a/F_o

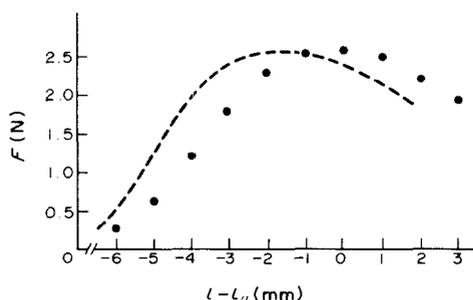


Fig. 4. Typical example of the force–length characteristics (rat no. 4). Points are measured at the muscle lengths indicated. The dashed line represents the force–length relation of the CE and was obtained by subtracting the SE-extension from the total muscle length at each force.

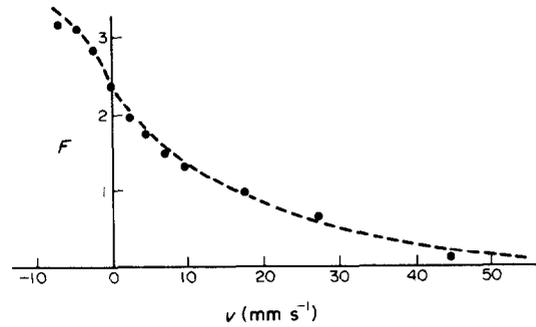


Fig. 5. Typical example of the force–velocity relation of rat no. 4 (dots). The relation was fitted by the dashed line (see text).

(Hill, 1970) was 0.20 ± 0.08 (Table 1). This value is within the normal range for these types of muscles (see Hill, 1970, for references), though it could have been higher if a higher temperature had been used (Ranatunga, 1984). In the eccentric part all three data points of course lie on the second order function which was used to fit these points. The response of the edl muscle on the two l_{O1} length–time functions is presented in Fig. 6 (dashed lines). The solid lines in this figure represent force output simulated on the basis of intrinsic properties of the muscle according to the model of Fig. 2 with blocked visco-elasticity.

If from all eight comparisons the maximal deviation between the two curves is divided by the amplitude of the actual force at the same instant, this maximal error appears to vary between 9.2% and 20% with a mean maximal error of 13.8%.

The errors show that properties of the muscles as measured in this study can to a large extent predict force output. There are however significant deviations. The experimentally derived force appears to continue to increase in the course of the eccentric phase which is much less the case in the simulated force while in the course of the concentric phase, the actual force shows a steeper decrease than the simulated one. Moreover at zero velocity (towards the end of the contraction) the force does not return to the level which it should have reached on the basis of its force–length characteristics. To some extent such a behaviour might be due to some visco-elasticity which is not measured in the quick release experiments. By means of systematic variation of both the proportionality constant k_v of the dashpot and the constant k_d of the elastic part of this visco-elastic element (see Fig. 2) it became apparent that a slight improvement could be achieved if a visco-elastic element with $k_d = 200 \text{ N s m}^{-1}$ and $k_v = 5 \cdot 10^6 \text{ N m}^{-2}$ was put in series with the undamped part of the SE. Figure 7 shows two examples of these simulations. At lower values for k_v (larger time constant) simulation yielded worse results; particularly the slopes of the force–time curves became less steep than in the experimental curves. This last finding supports the statement made by Hatze (1977) that the damping component of SE is small.

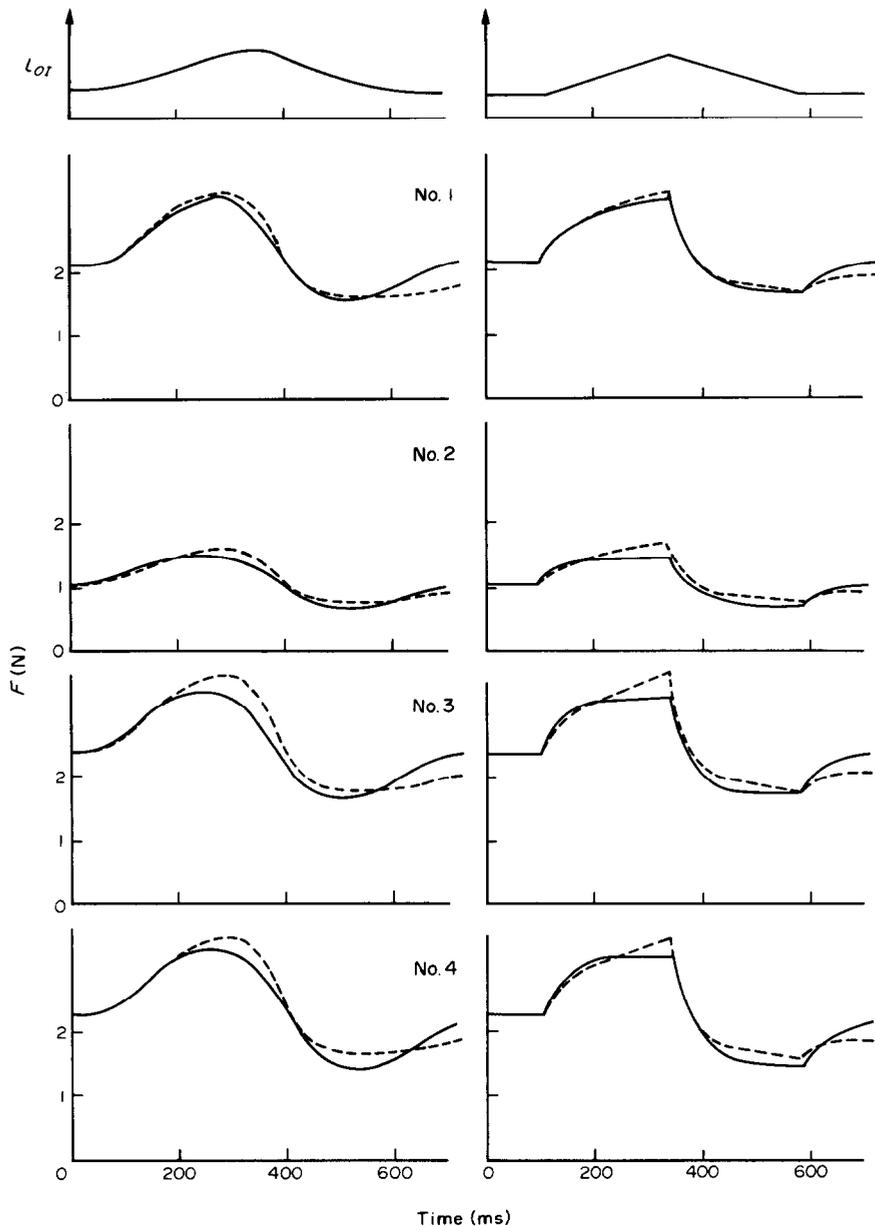


Fig. 6. Simulated force (solid lines) and experimental force (dashed lines) for different rats and two input functions (l_{OI}).

DISCUSSION

The simulation results (Fig. 6) show that within the applied range of muscle lengths and velocities (Fig. 1) a reasonable prediction of force output can be obtained on the basis of muscle properties defined by force-length, force-velocity and SE compliance characteristics. In particular if muscle force outputs are used to simulate movements of body segments, the order of magnitude of the deviations as shown in Fig. 6 will not lead to serious errors in the resultant velocity or position data of the limbs. Not the precise shape of the force curve but merely the mean force will be important when limb velocities and positions are to be

obtained by integration of the differential equations of the system.

If, however, one is interested in the precise nature of the production of force, positive and negative work of CE and SE and instantaneous power output, the results of this study show that important characteristics of the muscle are obviously not accounted for.

With this simple Hill-type model a few conclusions might be drawn with respect to SE characteristics. The simulations provide evidence for the reliability of the SE characteristics obtained by integration of the SE compliance to force. If distinctly more or less compliant SE's are used, the simulations lead to unrealistic results. Even when the k_s values of the four muscles are

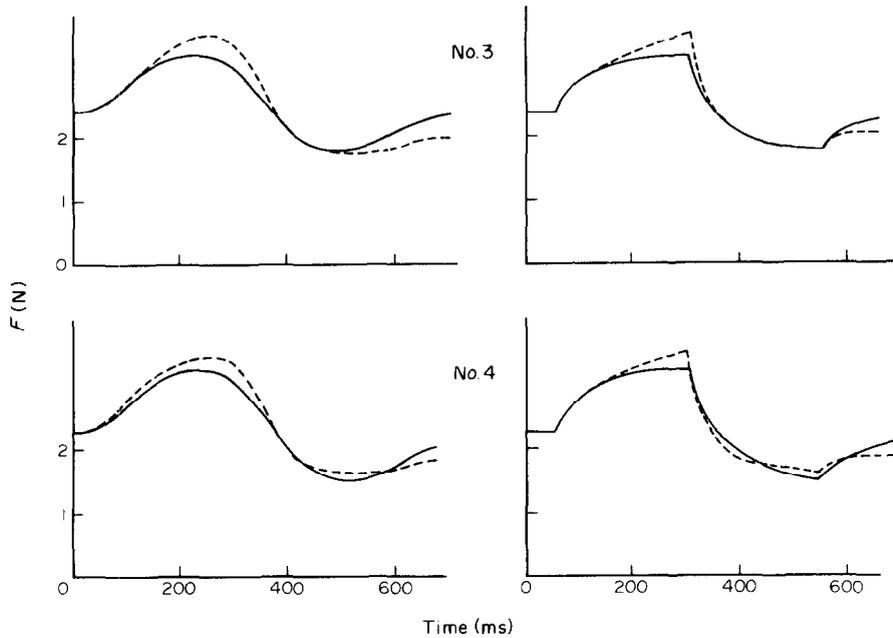


Fig. 7. Simulated force (solid lines) obtained with an undamped part of SE as used in Fig. 6 in series with a damped part.

exchanged, the simulations show considerably more deviation from the actual force response than what is shown in Fig. 6. With respect to this it should be noted that differences in SE compliance within the four muscles are relatively small with respect to the ranges of SE compliances assumed in the literature (see Ingen Schenau, 1984, for references). When expressed in SE extension at F_0 the lowest value of the present study was 3.0% while the highest value was 3.3% of l_0 .

Figure 7 shows that SE might also include a damped part though its influence is small (high stiffness). The slight improvement obtained by placing this visco-elastic element in the muscle, might in fact be the result of an artifact. Additional simulations performed with other curves fitted to the force-velocity data, appeared to lead to much better simulation results than the ones shown in Figs 6 and 7. If for example a function is used with an increasing slope at increasing negative values of v (Fig. 8), the simulation of magnitude, shape and slopes is strongly improved. Two examples of such results are presented in Fig. 9. Using these functions, visco-elastic elements do no longer improve the simulation results. Such manipulations with different curves showed that in particular the type of curve used in the eccentric part of the force-velocity relation, have strong influence on the entire simulation. If the slope of the curve increases at increasing eccentric velocities, the simulation is much closer to the experimental force output than if curves are used which are close to the actual data points which suggest a decreasing slope at larger eccentric velocities. This last phenomenon is always observed in this part of the force-velocity curve and is said to be due to slippage of the cross bridges.

Obviously force enhancement in the eccentric part

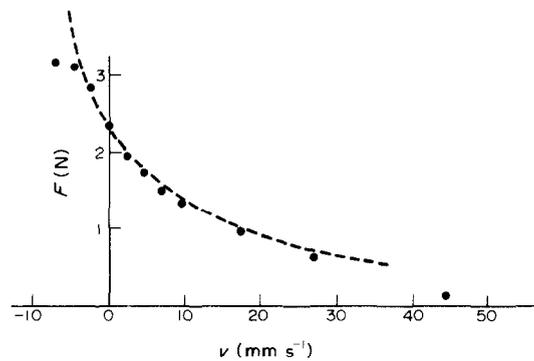


Fig. 8. A function (dashed line) of the form $v = A/(1 + B.F^C) - D$ with A , B , C and D as constants fitted to all points of the force-velocity relation of rat no. 4.

of the contraction during the movements illustrated in Fig. 1 is larger than the enhancement suggested by the data used to construct the force-velocity relation. This might at least in part be due to a difference in range of eccentric contraction. In the movements to be simulated, this range was most likely within the length range reported for the short range stiffness of approximately 1.7% of l_0 (Cavagna *et al.*, 1981; Morgan *et al.*, 1978). In the experiments performed to obtain the data for the force-velocity relation the length range of the eccentric contractions was larger with increasing eccentric velocities. At eccentric velocities higher than 2.5 mm s^{-1} the length range might have been larger than the length range at which the muscle begins to 'give' (Cavagna *et al.*, 1981). However, these differences in eccentric length ranges, which are the result of

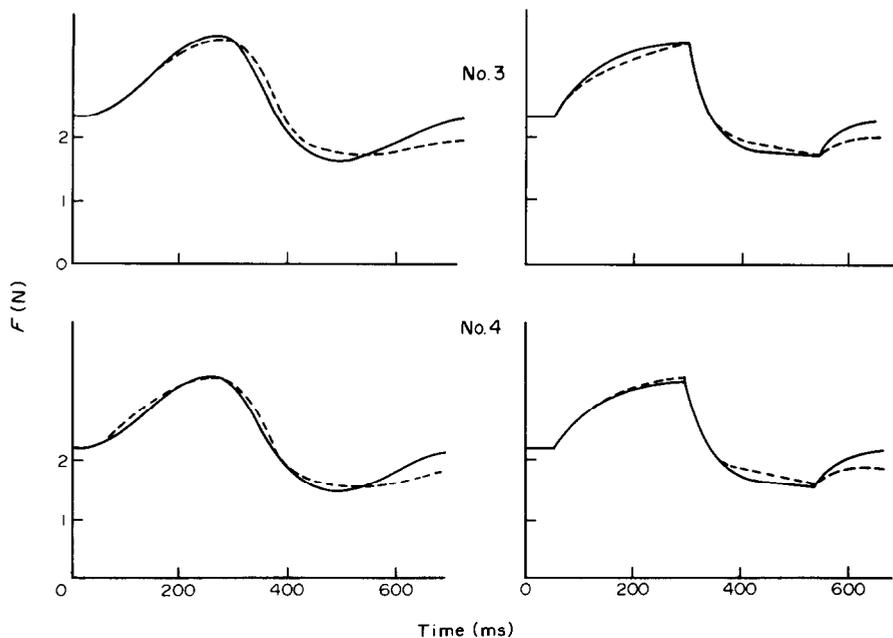


Fig. 9. Simulation results obtained by using the force-velocity function presented in Fig. 8.

choices explained in the methods sections, can not entirely explain the deviating simulation results since the forces measured during the eccentric contractions in the ranges where the muscle 'gives' are reported to be higher than the forces measured in the first part of the eccentric contraction (see for example Figs 2 and 4 in Morgan *et al.*, 1978).

This leads to a point which is probably more important within the scope of this study: the nature of the force-velocity characteristic of the muscle. In Fig. 10 two force-time functions are presented which were measured during the experiments performed to construct the force-velocity relation. The concentric and eccentric contractions (both at 5 mm s^{-1}) were simulated as well. These examples clearly show that the force enhancement in the course of the eccentric contraction can only be explained by the (simulated) SE compliance and force-velocity relation during the very first part of the contraction. Actually the increase in force continues until the termination of the eccentric velocity. The high force at the end of the eccentric phase can by no means be explained by elastic or visco-elastic elements. The same is true for the continuous decrease in force during the isokinetic concentric contraction.

Since the forces used in the force-velocity relation are the forces from these curves measured at l_o , the underlying properties of the muscle which might explain the slopes in the force-time curves of Fig. 10 are not incorporated in simulations based on force-length, force-velocity and SE characteristics. Although the phenomena expressed by Fig. 10 can be deduced from the results of several other studies (e.g. Abbot and Aubert, 1952; Cavagna *et al.*, 1968; Edman *et al.*, 1978), only few attempts have been made to

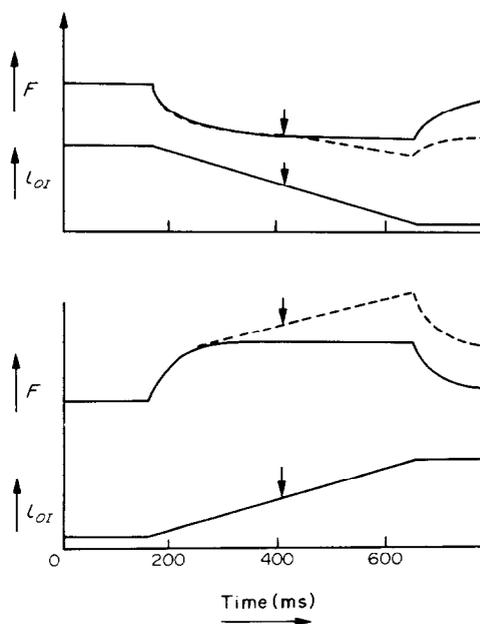


Fig. 10. In isokinetic concentric contractions (upper tracings) the experimental force (dashed line) shows a deficit which is not explained by intrinsic muscle properties defined by force-length, force-velocity and SE characteristics (solid lines represent simulated force). In isokinetic eccentric contractions (lower tracings) the experimental force appears to be stronger enhanced in the course of the contraction than what is predicted by the simulated force. The arrows indicate the instant at which $l_{OI} = l_o$.

incorporate them in Hill-type muscle models (Hatze, 1981b). At present it is not clear if this force enhancement and deficit can be regarded as phenomena which might be described independently from the

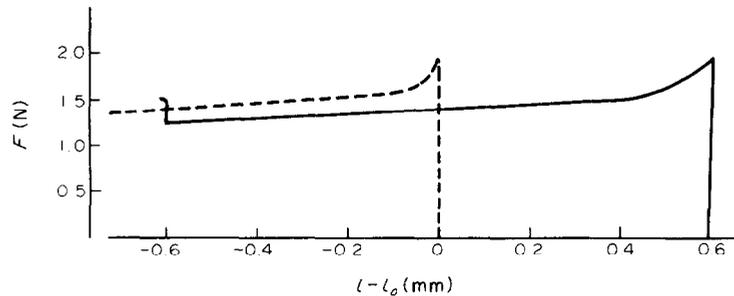


Fig. 11. Two force length diagrams of concentric muscle contractions of an edl, both performed at a velocity of 5 mm s^{-1} one starting at $l_0 + 0.6 \text{ mm}$ and the other at l_0 . Though in the overlapping length (-0.1 to -0.6 mm) the muscle had the same velocity and the same length, the force in the shortening with the longer history is smaller than the force in the contraction started at l_0 . The time of stimulation prior to the onset of concentric contraction was the same in both contractions.

force-velocity characteristics since the molecular basis for the interdependency of force and velocity is not unequivocally understood. Force enhancement during stretch seems not only to be dependent on velocity but also on muscle length (Abbot and Aubert, 1952; Atteveld and Crowe, 1980; Edman *et al.*, 1978). After a temporal increase of the number of attached cross bridges, the further enhancement of force seems to be the result of (a) a decrease of the number of attached cross bridges combined with forces per cross bridge considerably higher than the force per cross bridge which is found in isometric or concentric contractions, (b) longer attachment time per cross bridge than during concentric contractions and (c) progressive recruitment of strained cross bridges (Tsuchiya and Sugi, 1986; Cavagna *et al.*, 1985; Matsubara and Yagi, 1985). The deficit of force during concentric contractions is explained by the displacement *per se*, a shorter attachment time, a reduced number of attached cross bridges and a decrease in average force per cross bridge (Edman, 1975; Matsubara and Yagi, 1985; Ford *et al.*, 1985; Colomo *et al.*, 1986; Tsuchiya and Sugi, 1986). In addition to these phenomena it is known that the eccentric 'history' has an influence on force and work in the subsequent concentric phase (for as far as it is not explained by utilisation of elastic energy stored in the SE during stretch). This influence is called 'potentiation' of the muscle (Cavagna *et al.*, 1968), and seems to be a function of eccentric and concentric velocity, eccentric and concentric length range and average muscle length (Edman *et al.*, 1978; Cavagna *et al.*, 1981; Cavagna *et al.*, 1985). To make it even more complicated, this phenomenon is not only explained by a higher force after pre-stretch but also by a higher potential energy of the individual cross bridges which is not explained by cross bridge elasticity. This effect is called 'isoforce gain of energy' (Cavagna *et al.*, 1981, 1985).

With help of an additional experiment the influence of time history on force deficit during isokinetic concentric contractions is illustrated in Fig. 11. The concentric contractions were started at different initial muscle lengths but at the same stimulation pulse after

the onset of the stimulations. Figure 11 shows a difference in force at the same isokinetic contraction velocity and the same muscle length ($l_0 - 0.1$ to $l_0 - 0.6 \text{ mm}$). Obviously force is not only a function of eccentric history but also of concentric history.

Based on the referred literature as well as the present results it can be concluded that simple Hill-type models as used in this study are not suitable to account for these anomalies for the simple reason that there does not seem to exist one unique and instantaneous force-velocity relation (Jewell and Wilkie, 1958; Zahalak, 1981; 1986). A much more promising approach can be expected from Huxley-type models (Huxley, 1957; Julian, 1969; Julian *et al.*, 1974; Zahalak, 1981, 1986). In particular the recent study of Zahalak (1986) is convincing. In contrast to the Hill-type models, his model accounts for several of the effects described above. Moreover, these type of models provide a more direct relation to the liberation of metabolic energy and mechanical efficiency than the Hill-type models.

The Huxley-type models however are still rather complex and will require large computational efforts in simulating complex movement where many muscles are involved. Further simplifications of these models seem to be necessary before the Hill-type models will be abandoned by the biomechanics community.

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