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# THE FORCE–VELOCITY RELATIONSHIP AT HIGH SHORTENING VELOCITIES IN THE SOLEUS MUSCLE OF THE RAT

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## SUMMARY

1. In intact skeletal muscle fibres, estimates of unloaded shortening velocity obtained from slack test measurements ($V_0$) have been shown to exceed, by approximately 7%, estimates obtained from extrapolation of velocities measured during isotonic releases ($V_{max}$). In contrast, published values for the $V_0$ of whole soleus muscles of rats exceed $V_{max}$ by 56%. In the present study, we tested the hypothesis that this difference between whole muscles and single fibres is due to a difference in their respective force–velocity relationships at loads less than 5% of maximum isometric tetanic force ($P_0$). In addition, we examined, by computer simulation, the effect of inter-fibre heterogeneity on the force–velocity characteristics of a whole muscle.

2. The force–velocity relationship of soleus muscles of rats was determined at low loads, *in vitro* at 20 °C, by recording force maintained during controlled shortening at constant velocities. The relationship was simulated by assigning a hyperbolic force–velocity curve to each motor unit and summing the force contributions of individual units at each of a series of velocities.

3. When measurements from low loads were included, the force–velocity relationship intersected the velocity axis at $V_0$ ($5{\cdot}0 \pm 0{\cdot}1$ fibre lengths/s, mean ± S.E.M., $n = 10$), not $V_{max}$ ($3{\cdot}1 \pm 0{\cdot}1$ fibre lengths/s). The simulated and measured force–velocity relationships agreed at all loads, supporting the premise that the deviation from hyperbolic form responsible for the large disparity between $V_0$ and $V_{max}$ of whole muscles is a consequence of heterogeneity in shortening velocity among fibres.

## INTRODUCTION

A rectangular hyperbola fitted to velocities measured during isotonic shortening (Hill, 1938) provides a convenient description of the force–velocity characteristics of a skeletal muscle preparation. When loads are restricted to forces between 4 and 80% (Edman, Mulieri & Scubon-Mulieri, 1976) of maximum isometric tetanic force

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($P_0$), interpolation along the fitted hyperbola results in accurate estimates of the force–velocity relationship between measured data points. Extrapolation along the hyperbola to low loads (0–4% of $P_0$) has proven less accurate. Studies of the maximum shortening velocity of intact skeletal muscle fibres from the frog (Edman, 1979; Julian, Rome, Stephenson & Striz, 1986) indicate that $V_{max}$, the intersection of the fitted hyperbola with the velocity axis, underestimates by approximately 7% the velocity of unloaded shortening ($V_0$) determined independently with a series of step releases (the 'slack test'). This deviation was shown to be due to the non-hyperbolic nature of the force–velocity relationship at loads less than 5% of $P_0$ (Julian *et al.* 1986).

In whole soleus muscles from rats, $V_0$ exceeds $V_{max}$ by 56% (Claflin & Faulkner, 1985*a*), eight times the deviation expected based upon results from single frog fibres. However, Julian *et al.* (1986) have recently emphasized the uncertainty associated with estimates of $V_0$ in single-fibre studies and the importance of confirming those estimates with independent measurements. In that study, the progress of unloaded shortening following a step release was monitored photographically. The criterion for reading the duration of unloaded shortening from force records was chosen to correspond to the time at which the fibre became straight. In the absence of photographic calibration, $V_0$ values were found to vary by as much as 50% depending on the criterion used to read force records (Julian *et al.* 1986). Photographic confirmation of slack test results is not feasible when working with whole muscles.

The purpose of the present study was to test the hypothesis that the discrepancy between single fibres and whole muscles with respect to the ratio of $V_0$ to $V_{max}$ is due to a difference in their respective force–velocity relationships at low loads. The hypothesis was tested by extending measurements of the force–velocity relationship of whole muscle to the very low load range (less than 5% of $P_0$). These measurements were made by recording the force maintained during constant–velocity (isovelocity) releases.

Results from the isovelocity release experiments indicated that the force–velocity relationship of the soleus muscle was indeed different from that of single frog fibres at loads below 5% of $P_0$. It has been suggested (Hill, 1970; Claflin & Faulkner, 1985*a*) that a collection of fibres, each having a hyperbolic force–velocity relationship, could exhibit non-hyperbolic characteristics at low loads if the fibres were not homogeneous with respect to shortening velocity. We tested, by computer simulation, the potential for inter-fibre heterogeneity to contribute to the observed discrepancy between results from single fibres and whole muscles. Simulations were performed by assigning a hyperbolic force–velocity curve to each fibre of the soleus muscle based upon the distribution of motor unit contractile characteristics reported by Kugelberg (1976). Composite (whole-muscle) force–velocity curves were then generated by summing the force contributions of each motor unit at a series of whole-muscle velocities. The fit of the composite curve to the measured force–velocity data points was evaluated by summing the squared differences in the velocity dimension. The results of the isovelocity experiments have been reported in abstract form (Claflin & Faulkner, 1985*b*).

## METHODS

### *Contractile properties*

Experiments were performed on whole soleus muscles isolated from 4-week-old female rats (Sprague–Dawley). The rats were anaesthetized with an intraperitoneal injection of pentobarbitone sodium (50 mg/kg). Contractile properties were measured *in vitro* in a buffered physiological salt solution maintained at 20 °C and pH 7·4. Details of the apparatus and instrumentation have been described elsewhere (Claflin & Faulkner, 1985*a*).

Each muscle was subjected to a series of isometric contractions followed by a series of isotonic, step, and finally isovelocity releases. Isotonic and step releases were initiated at 100% and isovelocity releases at 105% of optimum fibre length. Optimum fibre length (hereafter termed 'fibre length') was defined as the length at which maximum isometric twitch force was elicited. Isotonic releases were performed at thirteen relative loads ranging from 5 to 50% of $P_0$. The data were fitted by a rectangular hyperbola of the form $(V+b)\ (P/P_0{}^* + a/P_0{}^*) = b(1+a/P_0{}^*)$, where $V$ is shortening velocity, $P$ is absolute load, the lines $P = a$ and $V = b$ are the asymptotes of the hyperbola, and $P_0{}^*$ is its intersection with the force axis (Hill, 1938). Values for the constants $a$, $b$ and $P_0{}^*$ were determined by hyperbolic least-squares regression of velocity upon load. To ensure that extrapolated $V_{\max}$ values were directly comparable to those from single-fibre studies, hyperbolae were not constrained to pass through the load axis at $P = P_0$ (Edman, 1979; Julian *et al.* 1986). The $V_{\max}$ was calculated as $V_{\max} = b/(a/P_0{}^*)$ and is reported in fibre lengths/s. Details of the procedure for determining $V_{\max}$ and $V_0$ have been described elsewhere (Claflin & Faulkner, 1985*a*).

The behaviour of the force–velocity relationship of the soleus muscle at loads between 0 and 5% of $P_0$ was determined by employing isovelocity releases. The isovelocity release technique has the advantage that measuring small forces is less difficult than applying small loads. Releases were performed during the plateau of a maximum isometric tetanic contraction, 500 ms after initiation of stimulation. Force was recorded during release from 105 to 95% of optimal fibre length at velocities ($V$) equivalent to $V/V_{\max} = 0{\cdot}40$, 0·50, 0·60, 0·85, 1·0, 1·1, 1·2, 1·3 and 1·4. Release velocities were further increased from $V/V_{\max} = 1{\cdot}4$ in increments of $V_{\max}/10$ until the level of force recorded during shortening reached zero. Further increments in velocity did not result in further decrements in force, but did induce slack as evidenced by a delay between the time at which the isovelocity release ended and force regeneration began. The minimum velocity of release required to produce zero force did not result in a time delay between the end of the release and the beginning of force regeneration. This velocity was designated $V_0'$. Releases performed on passive muscles at velocities equal to $V_0'$ also resulted in zero force, indicating that the small amount of passive tension present under static conditions at these lengths is damped to the extent that it is negligible during rapid shortening. Each isovelocity release was immediately preceded by a step release ranging in amplitude from 2·0 to 3·5% of fibre length. The effect of the step was to relax series elasticity to a level approximately consistent with the steady-state force produced during the subsequent period of isovelocity shortening (Cecchi, Colomo & Lombardi, 1978). The purpose of the step was to minimize transients in the force response during isovelocity release. The size of the step required increased as release velocity increased and force maintenance decreased. Steady-state force maintained during isovelocity release was not affected by the size of the preceding step. Force was measured when fibre length was 97% of optimum, approximating the fibre length at which velocities were measured during isotonic releases. Releases were initiated from a fibre length 105% of optimum to ensure that force measurements made at 97% were not obscured by transients. The $P_0$ was measured after every four to five releases. Forces were normalized by the most recently measured $P_0$. Measurements were separated by 2 min recovery periods. Records from a series of isovelocity releases are presented in Fig. 1.

After determination of $V_0'$, $P_0$ was measured again, passive tension at optimal length was determined and the muscle was blotted and weighed. The mean cross-sectional area of each muscle was estimated by dividing muscle mass by fibre length and the reported density of mammalian skeletal muscle, 1·06 g/cm$^3$ (Méndez & Keys, 1960).

Results are reported as mean ± 1 standard error of the mean. Student's $t$ test was applied to paired determinations of $V_0$ and $V_0'$ to assess differences at the 5% level of significance.

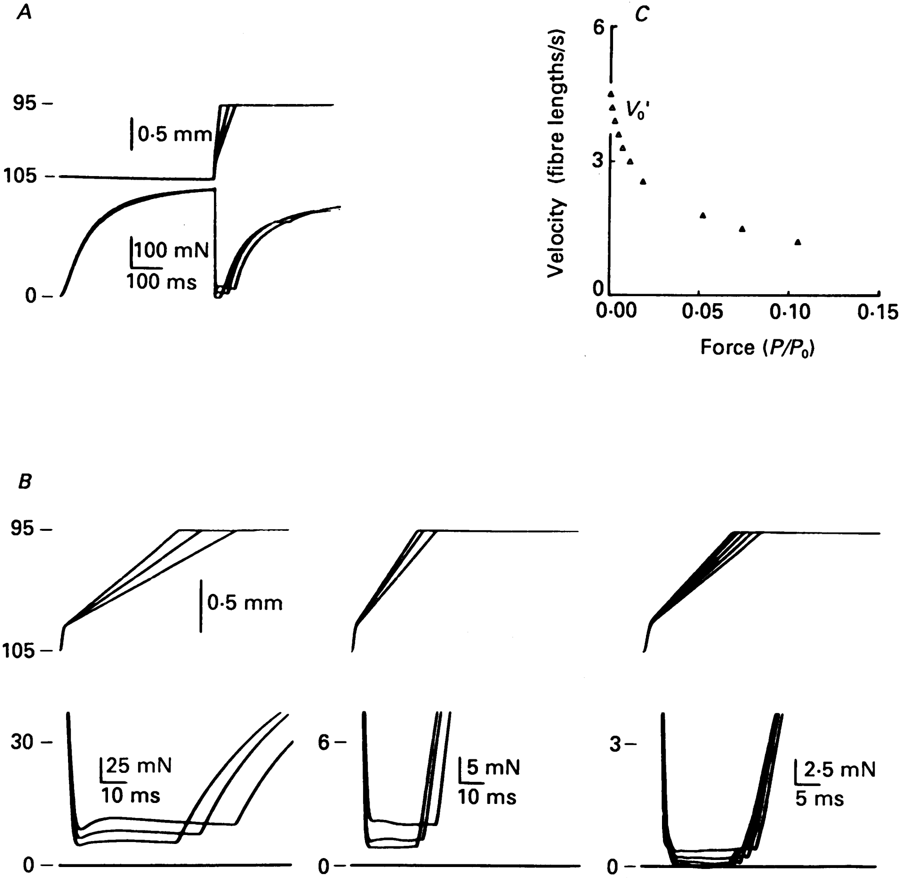

Fig. 1. Representative determination of minimum velocity required to produce zero force ($V_0'$) during isovelocity release. *A*, three representative isovelocity releases and resulting force responses. Velocities ($V$) depicted are $V/V_{max} = 0·40$, 0·60 and 1·40. Upward deflection of the oscilloscope traces indicates decreasing fibre length and increasing force. All muscles were released from 105 to 95% of optimal fibre length, indicated by the scale at the left of the displacement traces. *B*, magnification of a complete series of releases (upper traces) and force responses (lower traces). Release velocities were (left to right) $V/V_{max} = 0·40$, 0·50, 0·60, 0·85, 1·0, 1·1, 1·2, 1·3, 1·4, 1·5 and 1·6. Zero force was produced during releases at velocities of $V/V_{max} = 1·5$ and 1·6, the final two traces in the rightmost panels. Percentage of maximum isometric force is indicated by the scales at the left of the force responses. Time calibration bars refer to both displacement and corresponding force traces. *C*, symbols represent forces measured at time when fibre length was 97% of optimum. Absolute forces ($P$) were normalized by maximum isometric tetanic force ($P_0$) and plotted against release velocity. Note the expanded scale of the force axis. The $V_0'$ for this muscle was 1·5 times $V_{max}$ or 4·5 fibre lengths/s.

### *Simulation*

The force–velocity relationship of the soleus muscle of the rat was simulated by assigning a hyperbolic force–velocity curve to each of its motor units. In order to maintain a realistic simulation, each motor unit was assigned a hyperbola based upon the distribution of contraction times reported by Kugelberg (1976) for the soleus muscles of rats of similar age (Fig. 3*B*, inset). Force contributions of individual motor units were then calculated and summed at each of a series of shortening velocities, resulting in a composite force–velocity relationship for the whole muscle. The calculations were performed by digital computer.

In performing the simulation it was assumed that: (1) the force–velocity characteristics of single motor units are hyperbolic, (2) the intersection of each hyperbola with the velocity axis ($V_{\max}$) is inversely proportional to motor unit contraction time, (3) the curvature of each hyperbola (as indicated by the ratio $a/P_0$) increases with motor unit contraction time, (4) the maximum isometric force ($P_0$) generated by a motor unit is independent of its contractile speed, and (5) under circumstances in which the $V_{\max}$ of a motor unit is less than the velocity at which the whole muscle is shortening, that motor unit neither contributes to nor attenuates the force produced at the tendons by the faster motor units.

Assumption 1 is consistent with the purpose of the simulation; to determine whether the summation of contributions by a heterogeneous population of fibres, each having hyperbolic force–velocity characteristics, could result in a composite force–velocity relationship similar to that observed for the whole soleus muscle. Assumption 2 was based upon reports by Close (1964, 1965), that $V_{\max}$ and contraction time are inversely proportional in whole limb muscles. The assumption that this relationship exists at the motor unit level is supported by the lack of dependence of isometric twitch to tetanus force ratio on twitch contraction time among the motor units of rat skeletal muscles (Close, 1967). Assumption 3 was based upon observations that slow muscles (Katz, 1939; Close, 1964; Wells, 1965; Woledge, 1968; Wendt & Gibbs, 1974; Ranatunga, 1984;) as well as slow fibres (Lännergren, 1978, 1979; Lännergren, Lindblom & Johansson, 1982) demonstrate force–velocity relationships which are more curved (smaller $a/P_0$) than those of fast muscles or fibres. A linear relationship between $a/P_0$ and contraction time was chosen arbitrarily. The rationale for assumption 4 is provided by the absence of correlation between contraction time and $P_0$ among the motor units of the soleus muscle of the rat (Close, 1967; Kugelberg, 1976). The alternative to assumption 5, that non-contributing fibres present an internal impedance to shortening, was examined by including in some simulations an impedance factor proportional to all non-contributing motor units.

Each simulation began with the assignment of a force–velocity curve to each motor unit based upon assumptions 1, 2 and 3 and the distribution of contraction times among motor units of the rat soleus muscle (Kugelberg, 1976 and Fig. 3*B*, inset). The force–velocity curve of the whole muscle was then formed by summing the contributions of each motor unit, subject to assumptions 4 and 5, at each of a series of velocities ranging from 0 to the shortening velocity which resulted in zero force maintenance.

The composite force–velocity curve was fitted to the combined data from isotonic and isovelocity releases by varying three parameters: (1) the proportionality constant between the $V_{\max}$ values and the reciprocal contraction times of individual motor units, and (2) and (3), the slope and intercept respectively of the linear relationship between the $a/P_0$ values and contraction times of individual motor units. The combination of these parameters which resulted in the best fit of the composite curve to the data was determined by direct searching by computer. The criterion for best fit was mimimization of the sum of the squared residuals between the simulated curve and the twenty-four force–velocity means presented in Fig. 2.

## RESULTS

### *Contractile properties*

Physical characteristics and isometric contractile properties of the ten soleus muscles studied are presented in Table 1. The maximum isometric tetanic force measured after determination of $V_0'$ was $100 \pm 1$ % (mean ± S.E.M.) of that measured at the beginning of an experiment. Representative records from the determination of the $V_0'$ of one muscle are presented in Fig. 1. Data on shortening velocities and shortening forces are summarized in Table 1 and Fig. 2. Sums of squared residuals for hyperbolic fits to velocities measured during isotonic release in individual muscles were similar to that resulting from the fit to the means shown in Fig. 2. Straight lines accurately represented data from the slack tests; the smallest correlation coefficient

TABLE 1. Physical characteristics, isometric contractile properties and force–velocity characteristics of the rat soleus muscle ($n = 10$). Optimum fibre length was 0·71 of optimum muscle length (Claflin & Faulkner, 1985*a*). Values are mean ± 1 S.E. of the mean

| | |
|---|---|
| Muscle mass (mg) | 36 ± 2 |
| Optimal muscle length (mm) | 16·0 ± 0·3 |
| Passive tension at optimal length (mN/cm$^2$) | 88 ± 12 |
| Twitch contraction time (ms) | 90 ± 3 |
| Twitch force/$P_0$ | 0·22 ± 0·01 |
| $P_0$ (N/cm$^2$) | 16·2 ± 0·4 |
| $P_0{}^*/P_0$ | 1·19 ± 0·04 |
| Maximum rate of force development (%$P_0$/ms) | 0·89 ± 0·02 |
| $V_{max}$ (fibre lengths/s) | 3·1 ± 0·1 |
| $a/P_0{}^*$ | 0·075 ± 0·004 |
| $V_0$ (fibre lengths/s) | 5·0 ± 0·1 |
| $V_0{}'$ (fibre lengths/s) | 4·9 ± 0·1 |

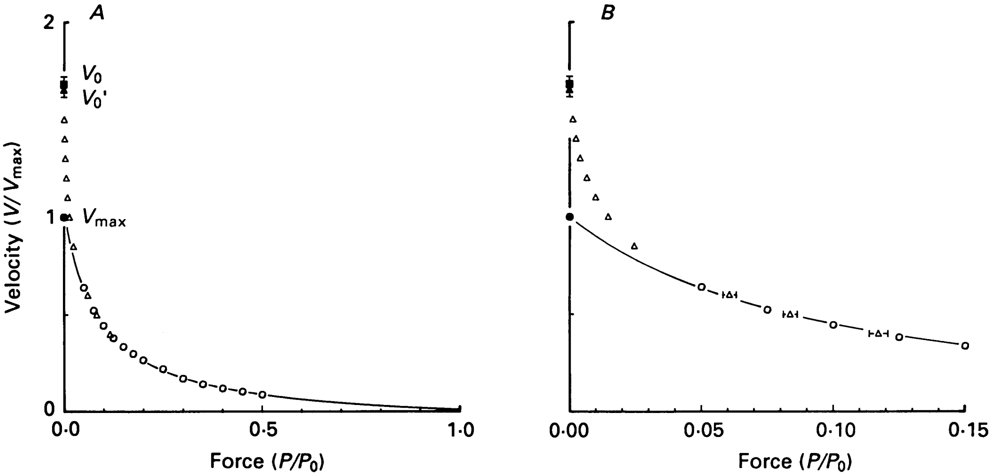

Fig. 2. *A*, mean isotonic shortening velocities and isovelocity shortening forces for ten soleus muscles. The filled square represents the mean $V_0$, velocity of unloaded shortening determined by the slack test. The filled triangle represents the mean $V_0{}'$, minimum velocity at which zero force is produced during isovelocity release. The open triangles represent mean forces maintained during isovelocity releases at each of ten relative velocities. Only those release velocities which did not exceed $V_0{}'$ in any of the ten muscles are represented. The filled circle represents the mean $V_{max}$, velocity of shortening at zero load extrapolated from velocities measured during isotonic releases. The open circles represent the mean isotonic shortening velocities at each load. The line represents the hyperbola which best fits the thirteen mean shortening velocities measured during isotonic releases ($V_{max} = 3·1$ fibre lengths/s, $a/P_0{}^* = 0·075$, $P_0{}^*/P_0 = 1·18$). *B*, as in *A* with expanded force axis. Absolute forces ($P$) are normalized by maximum isometric tetanic force ($P_0$). Error bars represent ± S.E. of the mean and are omitted where they fall within the mean symbol.

for the regression of the intervals of unloaded shortening upon release amplitudes for individual muscles was $r = 0·997$. Attempts to fit a rectangular hyperbola to pooled isotonic and isovelocity force–velocity measurements from individual muscles resulted in mean squared residuals approximately one-hundred times those of fits to measurements made exclusively by isotonic releases.

The 95% confidence intervals for means of forces produced at release velocities of $V/V_{max} = 0{\cdot}40$, 0·50 and 0·60 included points on the hyperbola fitted to means of velocities measured during isotonic releases. The range of loads over which isotonic measurements coincided with isovelocity measurements was approximately $P/P_0 =$ 0·12–0·05 (Fig. 2). Values for $V_0$ and $V_0'$ were not significantly different ($P > 0{\cdot}05$).

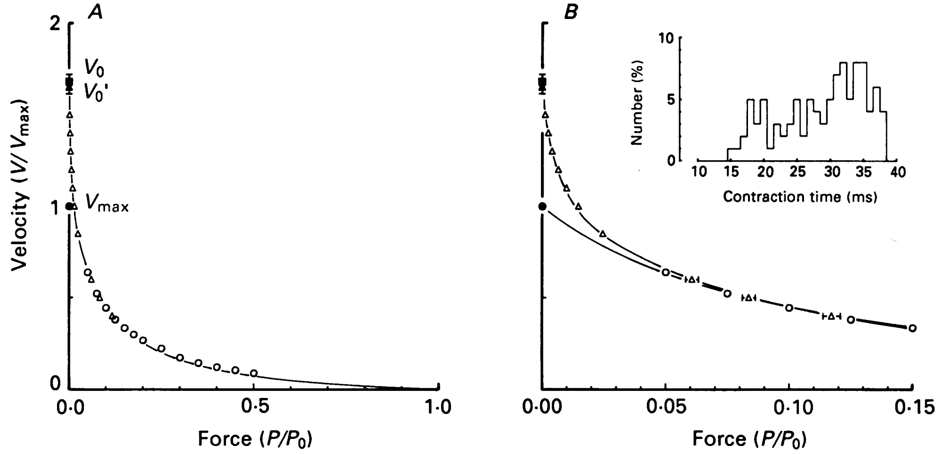

Fig. 3. *A*, simulated relationship which best fits force–velocity data from the soleus muscle of the rat. Force–velocity data points are as in Fig. 2. The line represents a summation of force–velocity hyperbolae, each hyperbola representing a physiologically distinct group of motor units (see text for details). *B*, as in *A* with expanded force axis. The lower line, included for contrast, represents the hyperbola which best fits the thirteen mean velocities measured during isotonic releases, as in Fig. 2. Inset, distribution of contraction times for motor units of the rat soleus muscle (redrawn from Kugelberg, 1976). In Kugelberg's experiments, measurements were made *in situ* on 5-week-old rats; muscle temperature was maintained at 36 °C; and distribution is based upon contraction times of 100 motor units from seven soleus muscles.

### *Computer simulation*

The best fit of the simulated force–velocity curve to the data occurred when the $V_{max}$ assigned to the motor units with the shortest contraction times was 1·95 times the $V_{max}$ of the whole muscle, the $a/P_0$ assigned to those motor units was 0·12, and the $a/P_0$ of the fastest motor units was twice that of the slowest (Fig. 3). An additional series of simulations was performed to determine the exclusivity of the values relating $V_{max}$ and $a/P_0$ to motor unit contraction time. Results from those simulations indicated that the fit of the simulated force–velocity curve to the data was unsatisfactory (sum of squared residuals greater than twice that of best fit) when the $V_{max}$ assigned to the motor units with the shortest contraction time was not within 5% of the best-fit value of 1·95.

The relationship between motor unit contraction time and $a/P_0$ was much less exclusive. Satisfactory fits were achieved with values between 0·08 and 0·12 assigned to the fastest motor units. Values between 1 and 2 for the ratios of the $a/P_0$ of the fastest motor units to the $a/P_0$ of the slowest were also consistent with a satisfactory fit. The values describing the relationship between motor unit contraction times and

$a/P_0$ were, however, pairwise exclusive. When the fastest motor units were assigned $a/P_0$ values from the low end of the range, a satisfactory fit was achieved only if the ratio between those values and the $a/P_0$ values assigned to the slowest motor units was also low. This relationship persisted through intermediate and high values within the range of satisfactory values for each parameter.

The model was modified slightly to test the effect of internal resistance due to non-contributing motor units. Instead of assigning a zero force contribution to each motor unit with a $V_{max}$ value less than the simulation shortening velocity, a force value equivalent to the weight (mass × acceleration due to gravity) of all non-contributing motor units was subtracted from the force sum. At high shortening velocities, the contributions of the fastest motor units were thus attenuated by the sum weight of motor units unable to 'keep up'. The curve resulting from this simulation was nearly indistinguishable from those which did not include an internal resistance factor.

## DISCUSSION

In single skeletal muscle fibres of the frog, the velocities of shortening at very low loads are slightly underestimated by a hyperbola fitted to velocities measured at higher loads (Julian *et al.* 1986). The magnitude of the error at zero load is approximately 7% (Edman, 1979; Julian *et al.* 1986). The present experiments indicate that, for whole soleus muscles of rats, shortening velocities measured at very low loads are severely underestimated by a hyperbola fitted to velocities measured at higher loads. The magnitude of the difference is 60% at zero load, more than eight times that reported in single fibres. A probable source of this discrepancy between single fibres and whole muscles is heterogeneity in shortening velocity among fibres of the whole muscle, the mechanism responsible being the loss of force contributions from slower fibres during shortening at the highest velocities. This hypothesis is supported by a computer simulation in which each motor unit of the soleus muscle was assigned a hyperbolic force–velocity curve and their contributions summed at a series of whole-muscle velocities. The resulting simulated force–velocity relationship of the whole muscle provided an accurate representation of the measured relationship.

### $V_{max}$

The $V_{max}$ extrapolated from a given set of force–velocity data points depends upon the technique for fitting the hyperbola as well as the range of loads over which measurements are made. In the present study, each hyperbola was fitted by minimizing the sum of the squared residuals in the velocity dimension. To be consistent with the studies on single fibres (Edman, 1979; Julian *et al.* 1986), hyperbolae were not constrained to intersect the force axis at $P_0$ and only force–velocity data from loads between 4 and 80% of $P_0$ were included. We conclude that the difference between the ratio of $V_0$ to $V_{max}$ from the present study (60%) and that from single fibres (7%) cannot be attributed to differences in curve-fitting techniques for determining $V_{max}$.

*$V_0$ and $V_0'$*

Julian *et al.* (1986) have stressed the necessity of calibrating the slack test with independent techniques in order to achieve reliable estimates of $V_0$. In whole-muscle preparations, the slack test cannot be calibrated photographically as described by Julian *et al.* (1986). Instead, the results of the slack test were verified independently by extending measurements of the force–velocity relationship of the soleus muscle through the low load range to the velocity axis. These measurements were made using isovelocity releases. At loads between 5 and 12% of $P_0$, the force–velocity relationship was assessed with both isovelocity and isotonic releases. Measurements made by the two techniques are in good agreement within this region, suggesting that the properties of the muscle being evaluated by isovelocity and isotonic releases are not different. The finding that $V_0$ and $V_0'$ coincide similarly suggests that both are measures of the same underlying processes. Thus, measurements made during isovelocity releases successfully span the very low load range, joining velocity measurements made during isotonic releases at loads greater than 4% of $P_0$ with those made at zero load using step releases. We conclude that our measurements of $V_0$ indicate accurately the intersection of the true force–velocity relationship and the velocity axis in the rat soleus muscle.

*Fibre type heterogeneity*

When each motor unit of the soleus muscle was assigned a rectangular hyperbola to describe its force–velocity characteristics and the contributions of the individual motor units were summed, the resulting relationship closely resembled force–velocity data obtained from whole soleus muscles. The fit of the simulated relationship was quite sensitive to the constant chosen to describe the relationship between $V_{max}$ and reciprocal contraction time at the motor unit level. The $V_{max}$ assigned to the fastest motor units was required to be within a few per cent of 1·95 times the $V_{max}$ of the whole muscle for an acceptable fit. This $V_{max}$ value for the fastest motor units is nearly 25% greater than results from step and isovelocity release experiments indicated.

The disparity between the $V_{max}$ of the fastest motor units required for accurate simulation and the $V_0$ of the whole muscle could result from the relatively small number of motor units having very short contraction times. Beginning with the shortest contraction times, the first significant 'cluster' in the distribution described by Kugelberg (Fig. 3*A*, 1976) and redrawn here (Fig. 3*B*, inset) represents motor units having contraction times of 18–20 ms. When the fastest motor units (contraction time = 15 ms) were assigned a $V_{max}$ of 1·95 (relative to whole-muscle $V_{max}$), the $V_{max}$ of the motor units within that cluster was 1·5–1·7 times whole-muscle $V_{max}$, ratios consistent with the current experimental results. It is possible that the sensitivities of the step and isovelocity release experiments were not sufficient to detect the small force contributions of the relatively small number of the very fastest motor units, allowing the more numerous motor units with contraction times from 18 to 20 ms to dominate the response. Alternatively, a slight attenuation due to slower motor units could have masked the contributions of a small number of very fast motor units at the highest shortening velocities. When an attenuating force equivalent to the weight of all non-contributing motor units was introduced, the effect on overall fit was insignificant; however, the effect on the intersection of the simulated force–velocity relationship with the velocity axis was sufficient in magnitude to explain the apparent disparity. Finally, a small deviation from hyperbolic form at the single-fibre level as seen in frog fibres (Edman, 1979; Julian *et al.* 1986) would have the effect of reducing or eliminating the disparity.

The simulated force–velocity relationship (Fig. 3) was achieved using a heterogeneous collection of single fibres with a distribution of individual force–velocity characteristics based on a unique distribution of motor units (Kugelberg, 1976). The agreement between the simulated and measured force–velocity relationships indicates that this distribution is sufficient to explain the force–velocity behaviour observed at low loads. No attempt was made to test whether the distribution used was a necessary condition for a good fit. The possibility thus remains that other fibre distributions, both simpler and more complex, could result in accurate simulations.

We have shown that the discrepancy between single fibres and whole muscles with respect to the ratio of $V_0$ to $V_{\mathrm{max}}$ cannot be attributed to curve-fitting technique or inaccurate estimates of unloaded shortening velocity for whole muscles. The results of the computer simulation are consistent with the hypothesis that the non-hyperbolic nature of the force–velocity relationship at low loads is primarily due to heterogeneity among motor units with respect to their force–velocity characteristics. Under this hypothesis, the steep slope of the force–velocity relationship at loads less than 5% of $P_0$ is a consequence of the decreasing pool of contributing fibres as the velocity of shortening of the whole muscle exceeds the maximum shortening velocity of an increasing number of motor units. A less likely possibility is that the discrepancy exists at the level of the single fibre. The applicability of these conclusions extends beyond the soleus muscle of the rat since other mammalian whole muscles display considerable heterogeneity (Close, 1967; Burke, Levine, Zajac, Tsairis & Engel, 1973; Garnett, O'Donovan, Stephens & Taylor, 1979; Edström & Larsson, 1987).

NOTE. While this manuscript was in review, Josephson & Edman (1988) published an account of the effect of fibre heterogeneity on the collective force–velocity relationship of a bundle of three fibres. The force–velocity relationship was determined for each of the three fibres and the force–velocity relationship of the bundle of three fibres was simulated based on the characteristics of the individual fibres. The simulated relationship was compared to the measured values for the bundle. Our conclusion is consistent with their conclusion that the ratio of $V_0$ to $V_{\mathrm{max}}$ is an index of the variability in maximum velocity of shortening among individual fibres in a muscle.

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