Force-Velocity Relation in Paired Frog Sartorius Muscles Attached to Opposite Lever Arms

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Abstract To study the mechanism of the longitudinal stability at the level of whole muscles, paired frog sartorius muscles were attached to the opposite lever arms at unequal distances from the pivot. The lever was initially fixed in position, and when the full isometric forces were developed in both muscles, it was released to move, the result being that the advantaged muscle shortened by stretching the disadvantaged one with a nearly constant velocity depending on the ratio between their points of attachment from the pivot. The force-velocity relation of the advantaged muscle was virtually identical with the ordinary force-velocity relation obtained from the isotonic release experiments, while the force-velocity relation of the disadvantaged muscle was found to be entirely different from the ordinary one because of a marked increase in the load-bearing ability. These results are discussed in connection with the enhancement of mechanical performance in lengthening muscle.

Key words: force-velocity relation, muscle contraction, load-bearing ability, longitudinal stability.

It is well known that the isometric tension in skeletal muscle is proportional to the amount of overlap between the myofilaments (GORDON et al., 1966). During the isometric tension development, the sarcomeres along the muscle length are not kept isometric; some sarcomeres shorten by stretching others. In spite of this nonuniform behaviour of the sarcomeres, no marked variation in sarcomere length takes place in isometrically contracting muscles; though the straight descending limb of the sarcomere length-tension relation (GORDON et al., 1966) is expected to produce a separation of widely divergent sarcomere populations (TER KEURS et al., 1979). A mechanism keeping the relatively small sarcomere length variation along the length of isometrically contracting muscle is called “longitudinal stability,” and is associated with the fact that stretched sarcomeres can bear more tension despite a decrease in the amount of filament overlap (e.g., EDMAN et al., 1978).
During the discussion in a symposium, Wilkie described a simple experiment done in A.V. Hill's laboratory, where paired frog sartorius muscles attached to the opposite lever arms at unequal distances from the pivot were stimulated to see the lengthening of the disadvantaged muscle by the advantaged one (WILKIE, 1979). The relationship between the advantaged and disadvantaged muscles may correspond with that between the adjacent sarcomeres, one shortens by stretching the other. As this type of experiment seemed so suitable for studying the mechanism of the longitudinal stability at the level of whole muscles, we used this method to examine the force-velocity relations of paired frog skeletal muscles, one of which shortened by stretching the other. It will be shown that the load-bearing ability of the muscle increases markedly when it is slowly stretched.

MATERIALS AND METHODS

Paired sartorius muscles (2.3–2.5 cm in length) isolated from one and the same frog (Rana nigromaculata) were mounted horizontally in two respective experimental chambers filled with Ringer solution (115 mM NaCl, 2.5 mM KCl, 1.8 mM CaCl₂, pH 7.2 by NaHCO₃). As shown in Fig. 1, their tibial ends were

![Diagram of experimental arrangement. Paired sartorius muscles (M₁ and M₂) attached at the tibial ends to the opposite lever arms (L₁ and L₂) which are pivoted at the middle, while the pelvic ends were connected to the force transducers (T₁ and T₂). The muscles were stimulated tetanically with repetitive current pulses through Pt plate electrodes (E₁ and E₂). When the lever is released by removing the stop (S), the advantaged muscle (M₁ in this particular case) shortens by stretching the disadvantaged one (M₂). The lever movement is sensed by the differential transformer (D). The point of attachment of M₁ to L₁ is fixed, while that of M₂ to L₂ is varied.](image)
attached to the opposite arms of an aluminium lever (11 cm in length) pivoted at
the middle, while their pelvic ends were connected to force transducers (Shinko,
type U, compliance 1 μm/g, resonance frequency of oscillation, 160 Hz). The
point of attachment of one muscle to the lever arm was kept 5 cm from the pivot,
while that of the other muscle varied from 0.5 to 5 cm from the pivot, so that the
lever arm ratio (i.e. the ratio of the distances from the pivot to the points of attach-
ment), ranged from unity to 10. The movement of the lever was sensed by a
differential transformer (Shinko, modulation frequency, 5.5 kHz). The temper-
ature of the Ringer solution was kept at 4–6°C, with the aid of a thermoelectric
device.

Each muscle at its slack length (L₀) was stimulated with 2 msec supramaximal
current pulses at 30 Hz, given through a pair of Pt plate electrodes (1 x 3 cm) at
both sides of the muscle. The lever was initially fixed in position with a stop, and
when the full isometric forces were developed in both muscles, the stop was quickly
removed electromagnetically to allow the advantaged muscle to shorten by stretch-
ing the disadvantaged one (one closer to the pivot). The force changes in both mus-
cles and the lever movement were simultaneoulsy recorded on an ink writing oscil-
lograph (Nihon Kohden, recticorder, frequency response, 100 Hz) (see Fig. 2).

To obtain the ordinary force-velocity relation, the experiments were also con-
ducted in the following manner: one of the muscles was replaced by loading springs
(5–10 cm in length) made of steel wires; when the stop was removed, the muscle
was allowed to shorten or lengthen according to the amount of isotonic load
imposed by the spring. All experiments were performed within the range of
muscle lengths where the resting tension was negligible.

RESULTS

Features of the mechanical interaction between the advantaged and disadvantaged
muscles

Figure 2 shows an example of the mechanical interaction between the paired
sartorius muscles attached to the opposite lever arms at unequal distances from
the pivot. When the full isometric forces (P₀) were developed in both muscles,
the lever was suddenly released by removing the stop. The release of the lever
caused a quick decrease in force in the advantaged muscle (Fig. 2A), and a quick
increase in force in the disadvantaged one (Fig. 2B). The initial quick displace-
ment of the lever coincident with these quick force changes (Fig. 2C) was due to
the elastic recoil of the series elasticity in the advantaged muscle and also to the
elastic extension of the series elasticity in the disadvantaged one.

Following the initial quick displacement, the lever started to move with a
nearly constant velocity, due to the shortening of the advantaged muscle by
stretching the disadvantaged one (Fig. 2C). For the first 200–300 msec after
the release, the forces in both muscles rose gradually (Fig. 2A, B). After this
period, the forces in both muscles became virtually constant. In the present study, attention was focused not on the initial quick lever movement, but on the subsequent steady lever movement.

**Force-velocity relations in the advantaged and disadvantaged muscles**

After the lever is released, the relation between the force in the advantaged muscle $P(t)$ and that in the disadvantaged one $P'(t)$ is expressed as $P'(t) = nP(t)$, where $n (>1)$ is the lever arm ratio. On the other hand, the relation between the velocity of shortening in the advantaged muscle $V(t)$ and that of lengthening in the disadvantage one $V'(t)$ is given as $V(t) = nV'(t)$. Thus, the force-velocity relations of the advantaged and disadvantaged muscles can be obtained by repeating the experiments, as is shown in Fig. 2 under various values of $n$. Since the force in each muscle reached a steady level at 200–300 msec after the lever release (Fig. 2A, B), the velocity of muscle length changes under the steady force ($P$) was determined by measuring the slope of the lever displacement trace at 200–300 msec after the release (Fig. 2C).

A typical result is shown in Fig. 3, where the force-velocity relations of the advantaged and disadvantaged muscles are compared with the ordinary force-velocity relation obtained by the isotonic release experiments. It will be seen that the force-velocity relation of the advantaged muscle is virtually identical with the ordinary force-velocity relation for forces smaller than $P_0$, while the force-velocity relation in the disadvantaged muscle is entirely different from the ordinary force-velocity relation for forces larger than $P_0$. In the isotonic release experiments, the muscle showed a tendency to lengthen rapidly when the amount of the

*Jap*nese Journal of Physiology
isotonic load was increased towards 1.8–2.0 $P_0$ (KATZ, 1939). In the disadvantaged muscle, on the other hand, the velocity of lengthening did not increase markedly, even when the force exceeded 2.5 $P_0$. Similar results were obtained with eight other muscles studied.

**DISCUSSION**

It has long been known that there is a discontinuity in the force-velocity curve between shortening and lengthening (KATZ, 1939). If the amount of isotonic load exceeds $P_0$, the initial slope of the relation between the load and the velocity of lengthening is much less steeper than that expected from the hyperbolic force-velocity relation, in the case of shortening muscle (HILL, 1938). With further increase in the amount of isotonic load towards 1.8–2.0 $P_0$, the muscle can no longer sustain it to be lengthened rapidly. This phenomenon is called “give,” and is generally interpreted as being due to the fact that each cross-bridge can not
bear a force twice as large as it generates (HUXLEY, 1960).

When we started the present work, we expected “give” of the disadvantaged muscle to occur if the lever arm ratio was large enough to give forces above 1.8–2.0 $P_0$ to it. As shown in Fig. 3, however, the disadvantaged muscle was found to bear forces above 2.5 $P_0$ while it was lengthening with a relatively slow velocity. The absence of “give” is obviously associated with the experimental condition in which the disadvantaged muscle is lengthened with a velocity smaller than the velocity of shortening in the advantaged one, depending on the lever arm ratio. This indicates that, when the load on the muscle is gradually increased, the load-bearing ability of the muscle markedly increases in comparison to the condition of isotonic release, where the load is rapidly increased.

The above time-dependent enhancement of the load-bearing ability observed in the gradually lengthening muscle may also operate at the level of the sarcomeres as the cause for longitudinal stability. During the isometric force development, the weaker sarcomeres (with a smaller amount of overlap between the myofilaments) would be lengthened relatively slowly by the stronger sarcomeres (with a larger amount of overlap). Thus the resulting enhancement of the load-bearing ability in the weaker sarcomeres would establish the longitudinal stability along the entire muscle length. The enhancement of the load-bearing ability in the lengthening muscle may be closely associated with the enhancement of mechanical performance observed after stretching or after isotonic lengthening (EDMAN et al., 1978; SUGI and TSUCHIYA, 1981a). The mechanism underlying these phenomena remains to be clarified, though some possibilities have been suggested (EDMAN et al., 1978; SUGI et al., 1984).

On the other hand, the force-velocity relation in the advantaged muscle was virtually identical with the ordinary force-velocity relation. This indicates that the shortening velocity at any one moment is primarily determined by the amount of load, irrespective of the past history of the shortening muscle. This is in accord with the results of SUGI and TSUCHIYA (1981b) that, in tetanized single frog muscle fibers, the shortening velocity for a given amount of load was the same, irrespective of whether the load was attained after a single force step or after two force steps with variable intervals.

REFERENCES


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