MECHANICS OF HUMAN ISOLATED VOLUNTARY MUSCLE

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The present report describes certain experiments made upon (essentially) isolated voluntary muscles of the human subject. Opportunity will also be taken to discuss certain matters of theoretical interest in muscle physiology.

MATERIALS AND METHODS

Four German amputees and two recently operated American amputees were available for the present study. These subjects, severally, had had cineplastic muscle tunnels placed through the flexors and extensors of the forearm, the biceps brachii, the triceps and a portion of the pectoralis major. Since these muscles had been freed from their bony insertions and deprived of their compensating skeletal lever arms, they were admirably suited for the study of muscle action. By insertion of pegs through the tunnels, affixed to stirrups, tensions developed by the muscles under various conditions were directly measurable. Furthermore, the activity of the muscles was produced by voluntary effort, and thus the pattern of neurostimulation was normal.

A new type of dynamometer was constructed to measure tensions, consisting of calibrated aluminum rings to which were affixed SR-4 type A-1 electrical strain gauges. The distortion of the rings was less than 0.001 inch for a force of 10 pounds. The gauges were connected in a conventional Wheatstone bridge arrangement so that all gauges were additive and the bridge self-contained on the ring. This type of connection reduced to a minimum the effects of temperature drift and external connection variations. The galvanometers used for recording bridge unbalances were Heiland type A, and the recording instrument was the Heiland type SE-301 R-12 oscillograph.

To control the possibility that the subject on approaching his maximal effort might unconsciously draw the extremity away from the dynamometer, an additional ring (compression ring) with affixed strain gauges was so placed as to record the reacting compression force from the distal end of the stump. Should no compression force be registered, it indicated that the subject was pulling away from the apparatus and that spuriously high tensions were being registered.

The experimental studies were divided into two groups: isometric muscle tension and isotonic (load-excursion) contractions.

1 These experiments constitute a portion of the Prosthetic Devices Research Project, College of Engineering, University of California, Berkeley, under contract VAm-21223, National Research Council, Committee on Artificial Limbs. The project was under the general direction of H. D. Eberhart, Associate Professor of Civil Engineering. Thanks are due to the many workers who participated in the research.
In the isometric studies the subject was placed in such a position that the dynamometer was in line with the direction of contraction of the muscle being studied. The adjacent bony parts were placed against the dynamometer so that compression could be recorded, and the peg through the muscle was connected by the stirrup and bicycle spokes to the aluminum rings. A turnbuckle and scale were inserted in the system in such a manner that passive changes in length of the muscle could be produced and measured. Recordings from the strain gauges could now be taken under conditions of passive stretch and under maximal voluntary contraction. Electromyograms, using surface electrodes, were routinely recorded. A rise of the integrated action potential to the same

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**Fig. 1. Strain gauge dynamometer.** Top and middle: arrangement for isometric studies. Bottom: adaptation for load-excursion studies.
maximum for successive runs assured equality of muscular effort. It was found
that there was good agreement (within about 10%) between the tension de-
veloped at a given length of muscle and the integrated action potential. Elec-
trical activity of muscle was never observed during passive stretch.

Load-exursion experiments were carried out on the same instrument, except
that the tension rings were removed and replaced by a pulley and light cable to
which was attached a weight pan. Increasing weights were added to the pan to
produce passive stretch. The subject rather slowly (2–5 seconds) lifted each
weight as far as possible and tried to maintain a uniform speed of contraction.

Details of the dynamometer and the experimental setup are shown in figures
1 and 2.
RESULTS AND DISCUSSION

1. The isometric length-tension diagram. Figure 4 shows the relationship between length and tension in the passively stretched (curve P) and the isometrically contracted (curve I) flexors of the forearm. Since the absolute lengths of the muscles were not known in the present experiments, the changes in length have been plotted, beginning with minimal length in the resting and contracted states. A third curve has been added (curve A), which is obtained by subtracting the passive tension from the isometric tension at corresponding lengths. This curve has been variously called the ‘contractile force’, the ‘developed tension’ and the ‘extra tension’ curve by previous investigators, and has been extensively discussed (1–7).

Blix (1), in his studies of frog muscle, pointed out that if the purely passive tension of a stretched resting muscle were independent of the additional force developed upon contraction (for which view he believed there was considerable justification), it followed that subtracting the passive curve from the isometric curve would yield a curve representing the contractile force. Pursuing this matter further, he showed that the A-curve exhibited a maximal value in the neighborhood of the ‘natural’ or resting length of the muscle, this being the length at which tension in the resting muscle first began to appear as the muscle was stretched. In figure 4 the resting length would correspond to the abscissal value 0.3.

It is evident that the Δ-curve of figure 4 reproduces the characteristics of the contractile force curve as described by Blix for frog muscle. Ramsey and Street (5) show the same type of curve for the isolated voluntary muscle fiber.
Ramsey (6) has recently tried to fit the $\Delta$-curve with a parabola. It is important to note, as Blix pointed out, that whereas the right-hand side of the $\Delta$-curve is obtained by subtracting two experimentally definable curves, the left-hand side, as customarily drawn, assumes that the passive tension is zero. Since, however, we know nothing of the passive tension below the resting length, the form of the left-hand side of the $\Delta$ curve is open to question.

It is of great physiological significance that the 'prosthetic length' in our subjects (that is, the length at which they liked to have their muscles placed in the artificial limb, and at which they felt they could exert the most force) corresponded closely to the resting length.

Figure 5 shows the isometric length-tension diagram for the pectoralis major. At first sight, the form of the $I$-curve seems very different from that in figure 4.

Had the experiment included measurements at much greater lengths, however, the $I$-curve would have started to rise again, in company with the $P$-curve. The pectoralis is remarkably extensible, in this experiment an elongation of over 4 inches being produced before the subject complained of discomfort. Within the range of lengths studied, the $P$-curve is so low that the $I$-curve and the $\Delta$-curve (not drawn) are practically identical. This constitutes an experimental justification for the view that the $\Delta$-curve is independent of the $P$-curve. As in figure 4, the maximum of the $\Delta$-curve occurs near the resting length.

Blix was much impressed by the variations in form which the $I$-curve of a given muscle exhibited in different physiological states (freshness, fatigue, etc.) and with different experimental techniques. The results shown in figures 3A and 3B, from Blix (we have added the $\Delta$-curves), were obtained by gradually loading a resting muscle, then tetanizing the muscle maximally and unloading it rapidly, but allowing time for the muscle to arrive at an equilibrium length at each successive load. The differences in the two $I$-curves Blix attributed, at least in
part, to fatigue. It will be observed that the $I$-curve of figure 3B shows a plateau like that of figure 4, but that the plateau is missing from the $I$-curve of figure 3A.

Blix pointed out that when the $I$-curve is obtained by the use of an isometric lever, there frequently occurs, especially if the muscle is fresh and vigorous, a secondary maximum and minimum in the curve. Such a curve is shown in figure 6, $I_3$, and in figure 7, the latter having been plotted from data given by Blix.

We explain these variations in form of the $I$-curve as follows: referring to figure 6, draw a typical passive stretch curve, $P$. Since all studies agree that the $A$-curve, representing developed tension, is convex upward, with a maximum near the resting length, we may draw a series of possible $A$-curves, each having the proper general form, but differing in maximal height ($A_1$, $A_2$, $A_3$). The lowest $A$-curve would correspond to a weak or fatigued muscle, the highest to a fresh or vigorous muscle. We may then construct a series of $I$-curves by adding the tensions of the $P$-curve to those of the respective $A$-curves. The resulting $I$-curves differ markedly in form, these various forms being similar to those observed experimentally (figs. 4, 5, 7). The particular form of the $I$ curve is, however, of no special physiological significance, aside from indicating the ability of the muscle to develop tension in excess of the passive tension.

Blix pointed out that the experiment of figures 3A–B (see description above) is incapable of revealing the presence of a secondary maximum and minimum.

During the course of preparation of this paper, we discovered that Buchthal (7) had given a similar explanation. Since his discussion was very brief, and not clearly implemented, we have felt justified in retaining the discussion in the present paper.
since each successive point on the $I$-curve represents a smaller load. This is an
elegant example of the subtle manner in which a particular experimental tech-
nique may alter the nature of the experimental results.

$I$-curves like those of figures 4, 5, 6 and 7 are of great physiological interest. The
presence of a plateau or of a secondary maximum and minimum is reminis-
cient of the ‘yield points’ described for certain engineering materials. Buch-
thal et al. (8) have suggested that ‘yielding’, in physiological muscular activity,
ensures constant contraction tension over a large range of stretch. We are of the
opinion, however, that this probably is not of as much importance in the intact
body as the nice compensation which occurs between the mechanical advantage
of joints in various positions and the forces exhibited by the muscles at those
positions. Thus, when the arm is extended, the mechanical advantage for
flexion is low, but the total force (contractile plus passive) which may be ex-
hibited by the flexor muscles is high. The reverse is true when the arm is moder-
ately flexed. In this connection, we may remark that the view sometimes ex-
pressed in the literature (for example Fenn, 9) that the resting length of muscles
in the body is practically the same as the maximal extended length, is certainly
not correct. Thus the resting length of the flexor muscles of the forearm cor-
responds to an angle at the elbow of approximately 90 degrees (10).

Buchthal and Kaiser (11) have found that the ‘dynamic stiffness’ of both the
resting and the contracted isolated muscle fiber is a linear function of tension.
Stiffness they define as $\frac{\Delta T}{\Delta L}$, where $T$ is tension and $L$ is length. $\frac{\Delta T}{\Delta L}$ is therefore
the slope of the tension-length curve. In their experiments they cause a muscle
fiber to minutely shorten and lengthen at a rapid rate (100 cycles/sec.) and
obtain therefrom a measure of the vibrational elasticity of the fiber, analogous
to the sonic elasticity of engineering materials. Their result, put in the notation
of infinitesimals, is that $\frac{dT}{dt} = $ constant. On integration, it follows that $L$
is a linear function of log $T$ (i.e., $T$ is an exponential function of $L$). We have
plotted $L$ against log $T$ for one of our smoothest and most complete passive
stretch curves ($P$ of fig. 4) and found that the points fall along a straight line.
This particular ‘static’ experiment, therefore, agrees with the ‘dynamic’ findings.

Schoepfle and Gilsun (12) have recently described an experiment on the re-
tractor penis muscle of the turtle, suggesting that the elasticity of active muscle
is the same, or nearly the same, as that of resting muscle at the same tension,
and have thereby been led to develop a transverse expansion theory of muscle
contraction. We do not wish to dispute this theory, since there may be a good
deal to be said in its favor. However, we do wish to call attention to the great
importance of examining in detail any experiment dealing with the elastic char-
acteristics of muscle. The study of muscle elasticity has been intensively
pursued ever since the time of E. Weber, a century ago, and anyone who reads the
literature on the subject cannot fail to be impressed by the vast inconsistencies
and contradictions in the results of the various investigators. Fenn (9), one of
the leading students of muscle physiology, has ascribed these discordant findings
to difficulties of interpretation. We should like to amplify this comment by saying that the particular muscle used, the conditions under which it is studied and the particular experimental technique employed are of absolutely critical importance in determining the results obtained. Blix was acutely aware of this. Referring to figure 6, it is clear that if we are working with a muscle at a length well above the resting length, we may expect to find closer correspondence between the elastic characteristics of the resting and contracted muscle than at shorter lengths, since the $I$- and $P$-curves approach each other at greater lengths. More than that, when the $\Delta$-curve is low, the $I$- and $P$-curves approach each other very rapidly. The data in the paper of Schoepfle and Gilson suggest that they were working in a region of the $I$- and $P$-curves where the slopes of the curves were nearly the same. Furthermore, it appears likely that quick-release experiments of the type under consideration may be self-defeating, because of the momentary disappearance of contractile force during the release.

2. The isotonic (load-excursion) diagram. Figure 8 shows the relation between load and shortening in the freely weighted pectoralis major. In constructing this diagram, the usual conventions of graphical representations have been violated in order to represent load and length in a manner similar to that of the preceding diagrams. It will be seen that under the conditions of the experiment, and with the range of loads used, the shortening bears a linear relationship to load. The straight line, when extrapolated out to zero shortening, yields a value for the load which agrees, within experimental error, with the maximal isometric tension as previously determined. The linear relation between load and excursion is true of the other muscles studied.

3. The load-work diagram. Figure 9 shows the load-work diagram for the muscle of figure 8. The curve is a parabola. In calculating the curve, values
of load and shortening were read off the straight line of figure 8, extrapolated out to zero shortening. It can easily be proved that a parabola will result, as follows: since load \((l)\) is a linear function of shortening \((s)\), \(l = ms + b\), the equation of a straight line, where \(m\) is the slope and \(b\) the \(y\)-intercept. Hence work = load \(\times\) shortening = \(s(ms + b) = ms^2 + bs\), which is the equation of a parabola. Since \(l\) is a linear function of \(s\), plotting \(ms^2 + bs\) against \(l\) must also yield a parabola.

**SUMMARY**

1. A new type of isometric dynamometer is described, in which muscle tensions are measured by strain gauges affixed to heavy metal rings and recorded oscillographically.

2. Isometric length-tension diagrams, load-exursion curves and load-work curves have been obtained for certain (essentially) isolated human muscles containing cineplastic muscle tunnels, under conditions of voluntary contraction.

3. It is shown that the isometric length-tension diagram and the load-work curve are similar to those previously described for frog muscle.

4. It is shown that the curve of developed tension has a maximum in the neighborhood of the resting length of the muscle, in agreement with earlier studies on frog whole muscle and single fibers. Attention is called to the lack of precise information concerning the form of the curve of developed tension below the resting length.

5. Variations in form of the isometric tension curve are discussed, and shown to be due to the variation in height of the curve of developed tension.

6. Evidence is provided that the curve of passive stretch represents an exponential function.

7. It is suggested that in studies of muscle elasticity, close attention should be paid to the region of the tension curves in which the muscle is being studied.

8. Under conditions of relatively slow and uniform speed of contraction, the excursion of the freely weighted muscle is shown to be a linear function of load, and proof is offered that a parabolic relation between load and work necessarily follows from this relationship.

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