

# The Variation of Muscle Oxygen Consumption With Velocity of Shortening

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**ABSTRACT** Total oxygen consumption following contraction at controlled shortening velocities was determined for ten twitches of frog sartorius muscle. Under the conditions of this investigation maximum oxygen consumption occurred at approximately 30 mm/sec. shortening velocity and decreased for larger and smaller velocities. Mechanical efficiency was calculated and found to show a maximum at approximately 20 mm/sec. shortening velocity. The relationship between this study and a similar investigation in which heat changes are measured as a function of shortening velocity is discussed.

## INTRODUCTION

Previous investigations on the relationship between oxygen consumption and work done by excised muscle have in all cases used load as the variable controlling the amount of work done. It has recently been pointed out (Hill, 1964 *b*) that experiments of this type involve an extra energy term, hitherto unrecognized. This term is the amount of heat liberated due to the persistence of tension after the load has been lifted and the shortening has finished. Hill designates the amount of heat so liberated as "*h*," the tension heat.

If the conditions of a twitch are arranged so that the tension at the end of the shortening phase is zero, then this term can be eliminated from the total energy equation (Hill, 1964). Using a device, such as a Levin-Wyman (1927) ergometer, which imposes a selected constant velocity of shortening, the requirement can be satisfied and variation of the speed will determine the work. Under these conditions the total energy liberated during a single twitch of frog sartorius muscle can be represented by the following equation:

$$E = A + W + ax$$

where:

$E$  = total energy liberated  
 $A$  = initial heat

$W$  = work done

$ax$  = "shortening" heat

The value of " $E$ ," the total energy, can be determined by a measurement of total oxygen consumption following a twitch at constant velocity (Baskin and Gaffin, 1965). The results thus obtained can be compared with the values obtained from heat measurement studies provided the mechanical conditions are similar in both investigations.

#### METHODS

Oxygen consumption was measured using a respirometer similar to that described by D. K. Hill (1940). Modifications were required in this respirometer in order to allow muscles to shorten under constant velocity. Certain of these modifications have been described in a previous paper (Baskin and Gaffin, 1965). Two rectangular chambers (each with a volume of about 6 ml) were connected at one end by a fine capillary tube. The other end of the chambers were connected by another capillary tube. This connection was controlled by a stopcock. In one chamber a single sartorius muscle was tied between two rigid holders. In the other chamber the matching sartorius muscle of the pair was clamped firmly at one end of a multigrad electrode system and tied to a steel wire at the other end. This steel wire was connected to a Levin-Wyman ergometer outside of the chamber through a fine hole which was enclosed by a mercury-filled well. An indicator liquid (kerosene) was used in the capillary in order to record the difference in volume due to the utilization of oxygen from the chamber containing the active muscle.

The capillary tube had a bore of 0.86 mm and sufficient sensitivity could be obtained for the measurements of oxygen consumption. With this technique it was possible to accurately measure the extra oxygen consumption resulting from ten consecutive twitches of the muscle. No permanent effect on the resting oxygen consumption of the muscle was noted as a result of such stimulation. (This is shown by the fact that oxygen consumption, after recovery, returns to its prestimulus level.)

The muscles were set at reference length using an isotonic lever and a 2 gm load. Tension generated during the shortening was measured using an RCA 5734 tube mounted at the end of the Levin-Wyman ergometer arm. Movement of the muscle was measured using a photocell and vane arrangement mounted on the ergometer arm. Tension and movement were monitored on a dual beam oscilloscope and recorded photographically. Velocity of shortening was determined by adjustment of the orifice in the Levin-Wyman ergometer cylinder.

One muscle of a sartorius pair (*Rana pipiens*) was mounted in each chamber of the respirometer. Both muscles were clamped at the pelvic end. The control muscle was fixed at reference length. The chambers were sealed and each chamber had inside it a strip of filter paper soaked in a 0.125 M solution of sodium hydroxide to absorb  $\text{CO}_2$  given off by the muscle. The respirometer was lowered into a temperature-controlled water bath and after the chamber had equilibrated at the desired temperature, the connecting stopcock was closed and the indicator bubble observed with a traveling micrometer. The extra oxygen consumption of a muscle following ten isometric twitches was first measured. The value determined was for ten twitches. The

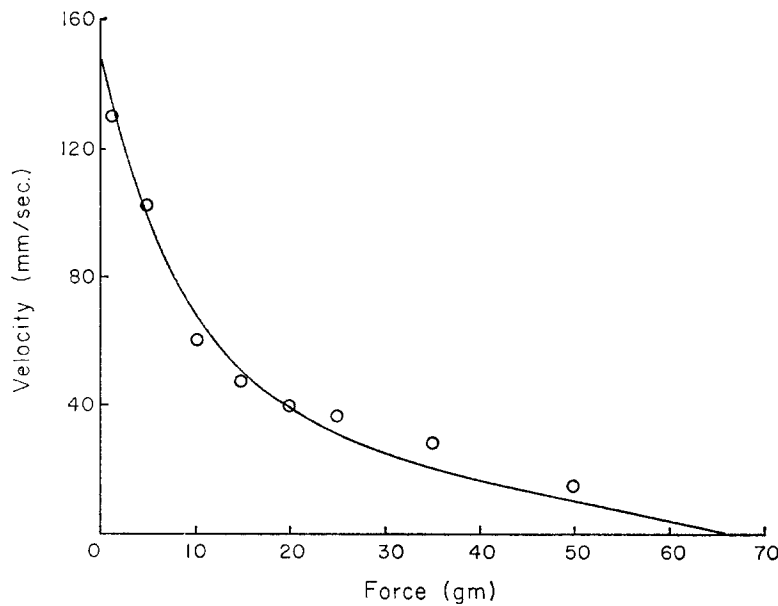


FIGURE 1. Force-velocity curve determined for the muscles used in this investigation. Muscle weight =  $140 \pm 5$  mg.  $L_0 = 37 \pm 2$  mm. Temperature =  $12^\circ\text{C}$ .

muscle was then given ten twitches at the desired velocity of shortening and total oxygen consumption measured. In order to avoid complications due to anoxia, only two runs were made on any one muscle. A given muscle therefore never received more than twenty twitches. This was not a sufficient amount of stimulation even to use up the oxygen originally present in the muscle (Hill, 1928). All the present experiments were performed at  $12^\circ\text{C}$ . The muscles used averaged 140 mg in weight and 37 mm in length.

The muscle was stimulated with ten, 4 millisecond rectangular pulses delivered at 1 second intervals. Shortening was started 6 milliseconds after the muscle was stimu-

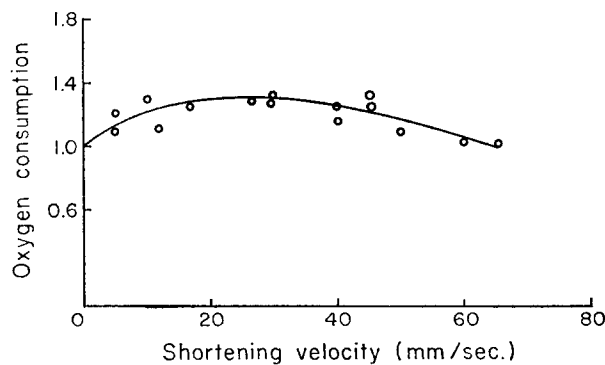


FIGURE 2. Total oxygen consumption plotted as a fraction of the isometric value at various shortening velocities. Temperature =  $12^\circ\text{C}$ .

lated. At each shortening velocity, the muscle was allowed to shorten 1 mm past the point of zero tension (see Figs. 3 and 4). Total oxygen consumption was determined from a graph of oxygen consumption *versus* time. (Readings were taken at 2 second intervals.)

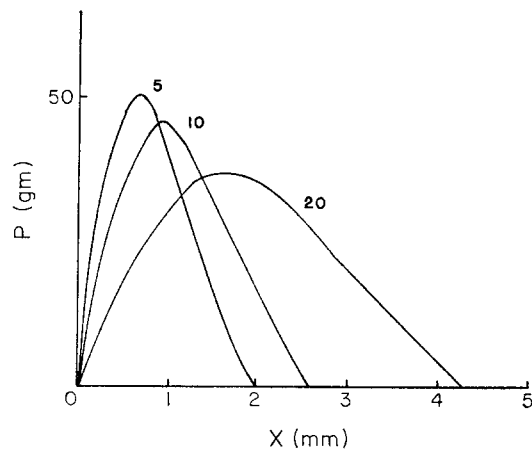


FIGURE 3. Tension plotted as a function of shortening for three shortening velocities, 5 mm/sec., 10 mm/sec., and 20 mm/sec.

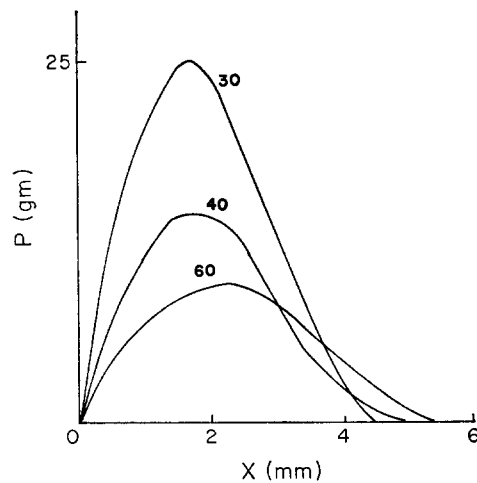


FIGURE 4. Tension plotted as a function of shortening for three shortening velocities, 30 mm/sec., 40 mm/sec., and 60 mm/sec.

A force-velocity curve was determined for muscles of the same size as used in the oxygen measurements. The curve obtained with after-loaded isotonic tetani is plotted in Fig. 1. Each point represents the average for six muscles. The muscles weighed  $140 \pm 5$  mg and were  $37 \pm 2$  mm in length.

#### RESULTS

Oxygen consumption, plotted as a fraction of the isometric value, is shown as a function of shortening velocity in Fig. 2. The curve has a maximum at about 30 mm/sec. and decreases for faster and slower velocities. Since a given

muscle was used only for one isometric and one constant velocity experiment, all the points represent data obtained from different muscles.

Total work done was obtained by graphical integration of the curves shown in Figs. 3 and 4. These curves show tension developed at a series of shortening velocities plotted as a function of distance shortened during the twitch. The calculated values of work for shortening velocities of 5, 10, 20, 30, 40, and 60 mm/sec. are listed in Table I.

TABLE I  
TOTAL OXYGEN CONSUMPTION AS A FUNCTION  
OF SHORTENING VELOCITY

Shortening velocity, mm/sec.	0	5	10	20	30	40	60
Total O <sub>2</sub> consumption, gm-mm	294	353	368	390	390	353	294
Work, gm-mm	0	55	66	95	56	35	28
W/total oxygen consumption	0	0.156	0.179	0.244	0.144	0.099	0.095

Temperature = 12°C. Data represent the average of values at each velocity.  $L_0 = 37 \pm 2$  mm.  $M = 140 \pm 5$  mg. Initial load = 2 gm.  $P_0 = 65 \pm 5$  gm.

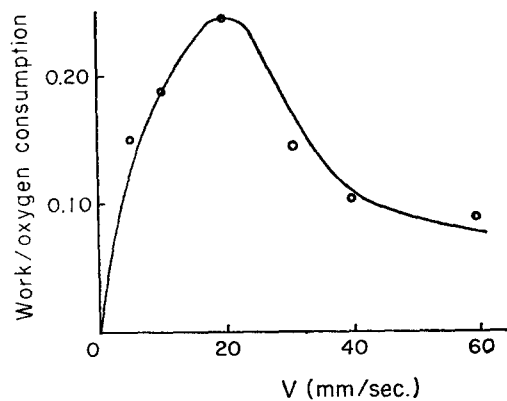


FIGURE 5. Mechanical efficiency ( $W$ /total oxygen consumption) plotted as a function of shortening velocity. Temperature = 12°C.

The ratio of work done to total oxygen consumption is shown as a function of shortening velocity in Fig. 5. The peak of this curve represents a large range of tensions (*i.e.*, from the force-velocity curve it can be seen that the range of 10 to 30 mm/sec. shortening velocity corresponds to a load range from about 25 to 50 gm).

Hill calculated initial energy as the sum of initial heat and work done, and mechanical efficiency as the ratio of work done to this initial energy. In the present study work is divided by total oxygen consumption to give mechanical efficiency.

## DISCUSSION

A discussion of studies on oxygen consumption in isolated muscle has been presented in other papers (Baskin and Gaffin, 1965; Baskin, 1965). None of these studies is directly comparable to the present investigation since load and not shortening velocity was the experimentally controlled variable. Hill (1964 *b*) has pointed out that the heat production and phosphocreatine hydrolysis studies of Carlson, Hardy, and Wilkie (1963) are open to a similar criticism. All these "work" *vs.* "total energy" studies include in the "energy" term a quantity  $h$  proportional to the tension but not specifically measured in the particular study. This term can be accurately measured only in those types of investigation which permit resolution of events occurring during a single twitch. At present only heat measurements permit this degree of resolution. With these factors in mind the "efficiency" *versus* shortening velocity curve is in approximate agreement with the curve shown in Hill's paper.

The magnitude of the energy demands of shortening could be estimated from the data obtained in this investigation, but its value would at best be a crude estimate since:

1. The value of total oxygen consumption at a given velocity of shortening was obtained for ten twitches and extrapolated to estimate the value for one twitch.
2. Shortening heat represents less than 15 per cent of the value of total energy. Since the total O<sub>2</sub> curve has been obtained by using a large number of different muscles, it is not sufficiently precise to make this calculation meaningful.

The results of this investigation show that a correspondence exists between the present oxygen studies and the description of muscle energetics which is obtained from heat measurements. Heat measurements have the advantage of speed of measurement and sensitivity. Oxygen studies, however, are of value in determining muscle energy changes in those muscles which for anatomical reasons cannot be precisely investigated by the method of heat measurement.

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