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The Force-Velocity Curve of Striated Muscle.

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When the force which is exerted by a muscle is plotted, on the ordinates, against the speed with which it shortens, on the abscissae, the curve relating the two variables is, in general, a straight line sloping towards the x axis. This relationship between force and velocity means that the force exerted by a muscle diminishes as its speed of contraction increases. This result has appeared in the work of Gasser and Hill,¹ Fenn² and in our own experiments soon to be published at length elsewhere. The purpose of this paper is to report a fact which emerges from our data which seems to throw light on the cause of the force-velocity relation.

Our experiments were made on the gastrocnemius muscle of the decerebrate cat stimulated through the tibial nerve by a single maximal, break, shock of a Harvard inductorium. The muscular response was, therefore, a twitch. The muscle contracted against an inertia disc (radius 8.65 cm.) the moment of inertia of which was 290,400 gm.-cm.² The displacement of the disc was recorded optically. Time was imprinted on the record in intervals of .001" by means of a slotted disc which was rotated by a synchronous motor in such a way as to interrupt a thin beam of light from a 500 watt lamp. The displacement of the inertia disc was measured from the photographic record with a cathetometer for each .001" and from these measurements, by taking first and second differences, the angular velocity and angular acceleration of the disc were computed. Although this record was measured to each .001", we have used in this computation, the interval of .01". The force, calculated from the moment of inertia and the angular acceleration of the disc, is, therefore, known for each time interval (.01") during the contraction cycle. The shortening of the muscle was also simultaneously and independently recorded on the same record by means of a fine steel wire which drew, in a straight line without magnification an aluminum pointer in front of the camera as the muscle contracted. The change of length of the muscle for each .01" was measured in the same manner as that described above for the measurement of the

¹ Gasser and Hill, *Proc. Roy. Soc., B.*, 1924, **96**, 398.

² Fenn, Brody and Petrilli, *Am. J. Physiol.*, 1931, **97**, 1.

angular velocity of the inertia disc. From the measurement of the change of length of the muscle for each .01" the linear speed of contraction of the muscle for the same time interval was obtained. The force of the muscle, the speed with which it contracts and the shortening of the muscle in cm. are, therefore, known for each .01". From these basic data, the work and power of the muscle for each time interval have been computed.

In Table 1, are presented the results of a single experiment on Cat 474 Record 3 which is typical of the twitch in a series of 20 animals. This animal was a pregnant female which weighed 2.8 kg. The length of the muscle was 9.5 cm. under an initial tension of 226 gm. Column 1 gives the time intervals in .005" in order to allow the data to be arranged in the table as they should be plotted on the time scale. Velocities are placed on the half hundredths because the values are the average velocities over the whole period of .01". Columns 2 and 3 give the muscle shortening in centimeters and also the change of length for each .01". Column 4 gives the linear muscle velocity in cm/sec. Column 5 gives the angular velocity of the disc in radians/sec. Column 6 gives the angular acceleration of the disc in radians/sec.² and column 7 the force in kg. Force in dynes is computed by multiplying the moment of inertia of the disc by the acceleration and dividing this product by 8.65 cm., the radius of the disc. Force in dynes is converted into force in kg. by dividing the former by 980,000. The term power is used in its technical signification which means the rate at which work is done. Power is equal to the work done in unit time divided by the same time interval and it is also equal to the force exerted in unit time multiplied by the corresponding muscle velocity. Power, Column 9, is the product of force, Column 7, and muscle velocity, Column 4. The figure for the muscle velocity is obtained by taking the average of 2 adjacent values to find the muscle velocity which corresponds in time to the force in Column 7. This figure is the figure in brackets in Column 4. Work, Column 8, is obtained by multiplying the figure for power by .01".

The fact brought out by these experiments, which is significant for the interpretation of the force-velocity curve is the approximate constancy of power (Column 9) after the muscle has attained its maximal force. $\text{Power} = \text{Force} \times \text{Velocity} = \text{a Constant}$. It follows from this equation that force and velocity vary inversely. Therefore, if velocity increases, force must necessarily diminish. The inference, therefore, appears to be warranted that in the work cited above, the force-velocity relation obtains because muscles move

during a part of their cycle under constant power. In none of the work hitherto published was the speed of the muscle independently and simultaneously recorded so that it has not been possible to compute from that data the power of the muscle from moment to moment during contraction.

It may be pointed out that the fact that muscle contracts under approximately constant power, after maximal tension has been developed, lends some weight to the theory that there are 2 sources of energy in a contracting muscle: an electro-chemical source which contributes the sudden development of maximal tension within the first 30 sigma after stimulation and an elastic source which absorbs the initial outburst of energy and delivers it at such a rate that the muscle does its work under constant power.

TABLE I.

1	2	3	4	5	6	7	8	9
Time in .005"	Muscle Shortening, cm.	Change of Length of Muscle per .01", cm.	Muscle Velocity cm./sec.	Angular Velocity of Disc rad/sec.	Angular Acceleration of disc rad/sec. ²	Force, kg.	Work, kg./cm.	Power=f v
0	0	0	0	0	0	0	0	0
.0025"			[2]		70.0	2.400	.048	4.80
.005"			4	0.34				
.010"	.04	.04	[7.5]		93.0	3.180	.238	23.82
.015"			11	1.27				
.020"	.15	.11	[13]		46.0	1.580	.205	20.54
.025"			15	1.735				
.030"	.30	.15	[15]		34.5	1.180	.177	17.70
.035"			15	2.08				
.040"	.45	.15	[15.5]		35.0	1.199	.185	18.58
.045"			16	2.43				
.050"	.61	.16			00.0			
.055"			12	2.43				
.060"	.73	.12						