

EFFECT OF LOAD AND INITIAL LENGTH ON THE WORK OF THE MUSCLE TRABECULA

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According to Starling's law [10], the mechanical energy liberated by the contracting myocardium is determined by the diastolic volume of the heart or the diastolic length of the myocardial fibers.

The hemodynamic demands resulting from an increase in the venous return or from a relatively high arterial pressure to be overcome by the heart during the systolic expulsion of blood may naturally be satisfied by a preliminary increase of the diastolic volume. Correspondingly, a small load (a relatively low arterial pressure) may be overcome at a small diastolic volume and minimal initial length of the fibers.

Leaving aside for the moment the possibility of increasing the strength of systole by direct trophic neuro-humoral influences on the myocardium [1, 5-9], we must assume that the necessary increase in the strength of systole required in these conditions may be brought about by an automatically regulated increase in the initial length of the fibers. It has not been proved experimentally, however, that a lengthened myocardial fiber is capable of greater work and of overcoming a larger resistance or load. The working effect of the trabeculae was therefore studied during the application of different loads, in relation to their degree of stretching.

EXPERIMENTAL METHOD

Experiments were carried out on isolated trabeculae from the atrium of the frog *Rana temporaria*. The large longitudinal trabeculae from the right atrium (from 1 to 3 in a preparation), forming a parallel bundle, were used. The initial length of the trabecular preparation varied from 4.0 to 4.5 mm (i.e., the length of the trabecula in the resting period, when attached to a lever strictly balanced at the horizontal level, and not under tension from an external force).

The mechanical activity of the trabeculae was recorded on a kymograph by means of a light glass pen, attached to the trabeculae by a ligature. Besides the contractions of the trabeculae, the resting and action potentials were recorded. The potentials were picked up by Dubois-Reymond nonpolarizing electrodes and fed into a type ÉNO-1 electron beam oscillograph. The potentials observed on the screen of the oscillograph were recorded by connecting the amplifying system and the preparation itself to a type MPO-2 loop oscillograph. The trabeculae were kept at a given, constant length during variations in the load by means of a supporting micrometer screw, which takes the weight of the lever at rest and during relaxation of the trabecula. The micrometer screw may be set at any desired level and the trabecula may thus be stretched to a precisely determined degree. The method of graduating the amount of stretching of the trabeculae was described fully elsewhere [2].

The contractions of the trabeculae with different loads and depending on their degree of stretching were re-directed as follows. At first an initial load was suspended (differing in each experiment, depending on the number of trabeculae in the preparation), after which an initial very slight stretching of the trabeculae was carried out (usually by 1.1% of its initial length), without which the trabeculae would be incapable of performing externally visible mechanical work [2]. The trabeculae were then gradually stretched to the maximal length attainable with this particular load. The trabeculae were then returned to their initial position, the load was increased, and the trabeculae were again stretched to their maximal length with the new, increased load. The increase in the load and in the associated degree of stretching was continued until the work of the trabeculae began to decrease as a result of excessive stretching at the maximal load for that particular preparation.

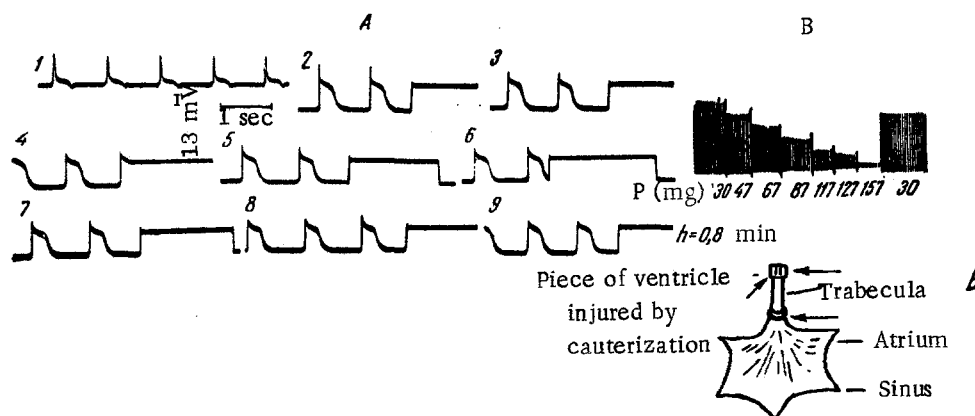


Fig. 1. Electrical (A) and mechanical (B) activity of trabeculae depending on changes in load in isometric conditions (20% of initial length). Scheme of recording electrical activity of trabeculae (C). Preparation of 3 trabeculae. Initial length 4 mm.

Two series of experiments were conducted. In the first (30 experiments) the work of the trabeculae was studied during stretching to a constant degree and with an increasing load. The object of this series of experiments was to determine the optimal loads (the maximal working effect) at that particular constant length. In this case the load could be regarded as analogous to the arterial pressure counteracting systole. In the second series (20 experiments) the work of the trabeculae was studied during an increasing load in relation to the maximal length attained with each load. As a control of the effect of stretching on the work of the trabeculae, measurements were made of the work done by each of these trabeculae at the given, constant, initial length.

EXPERIMENTAL RESULTS

Curves showing the relationship between the mechanical and electrical activity of the trabeculae and an increasing load at a constant initial length are shown in Fig. 1 (results of one typical experiment). The trabeculae were preliminarily stretched by 0.8 mm, corresponding to 20% of their initial length.

To facilitate analysis of the mechanical work performed by the trabecula in relation to the load during isometric contraction, the graph in Fig. 2, is provided.

As the load increased, the work of the trabecula gradually rose to a limiting level and then fell gradually to zero. The magnitude of the resting potential fell with an increase in the load from 42 mV initially to 36 mV at the end of the experiment (by 14.3% of the initial value). The amplitude of the action potential also fell slightly – from 52 to 48 mV at the end of the experiment (by 5.8% of the original value). The form and duration of the action potential remained unchanged (Fig. 1, A).

At the moment when, because of excessive loading, the work of the trabecula fell to zero no external sign of contraction was visible. At this time, the electrical activity of the trabecula was completely preserved with no change in the shape and duration of the action potential. Under these circumstances the magnitude of the resting potential and the amplitude of the action potential diminished, although only very slightly (Fig. 1, A, 8). The numerical results are summarized in the table.

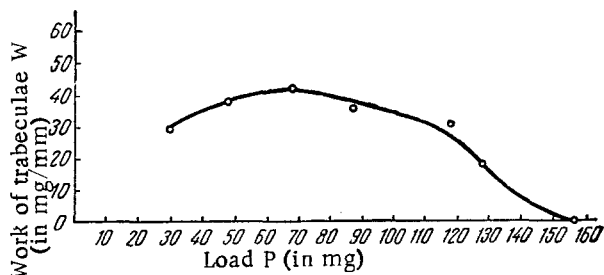


Fig. 2. Graph showing changes in working effect of trabeculae depending on an increasing load at constant length (20% of original). Preparation of 3 trabeculae. Initial length 4 mm.

After the relationship between the working effects of the trabecula and the load at constant length (20% over the initial value) had been determined, it was necessary to find the relationship between the work done and the increasing load and also between the work done and the lengthening of the trabecula at rest. The trabecula was stretched to the maximal length corresponding to each load. The curves of three typical experiments of this series are given in Fig. 3.

Absolute Magnitudes of Changes in Working Effect (W), in the Value of the Resting Potential (RP) and in the Amplitude and Duration of the Action Potential (AP and DAP) (Experiment 40 on Nov. 14, 1961. Preparation of 3 Trabeculae. Initial Length 4 mm)

h (in %)	P (in mg)	H ₁ (in mm)	W (in mg/mm)	in mV		DAP (in sec)
				RP	AP	
0,8	30	1,0	30,0	42,0	52,0	0,66
20,0	47	0,8	37,6	40,0	52,0	0,66
	67	0,63	42,0	37,5	52,0	0,66
	87	0,42	36,0	37,5	51,2	0,66
	117	0,26	31,0	37,0	51,2	0,66
	127	0,16	19,0	36,0	50,0	0,66
	157	—	—	36,0(14,3%)	49,0(5,8%)	0,66

Legend: h — degree of stretching, H₁ — true shortening of trabeculae

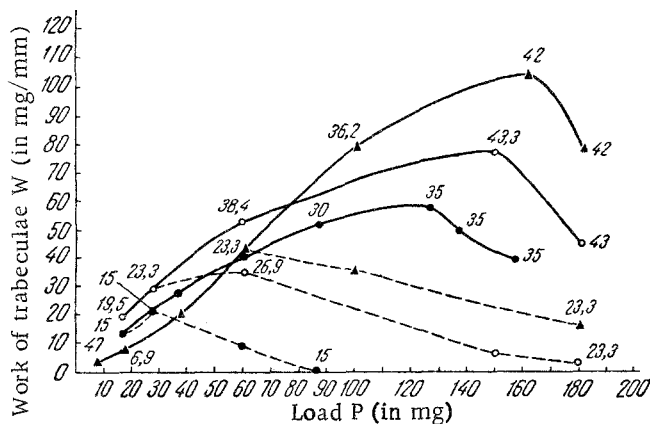


Fig. 3. Work of trabeculae at different loads during an increase in the initial length (continuous lines) and with different loads but at a constant initial length (broken lines). The length of the trabeculae for each load is maximal. The numbers on the curves indicate the degree of stretching for each trabecula (in %).

Measurements were made by means of a special measuring arc and tension pick-up. An increase in the initial length of the muscle segment between the two points of attachment of the measuring arc by 30% was found to lead to a significant increase in the strength of the contraction. At the same time, these workers also established that a direct relationship exists between the strength of contraction and the arterial pressure.

We consider that the changes in the strength of the contractions of the trabeculae depending on the load during an increase in the "diastolic" length, in our experiments, are analogous as regards their initial conditions to the changes in the strength of the contractions during an increase in the arterial pressure.

SUMMARY

A study was made of the changes occurring in trabeculae during working effort in response to various loads in relationship to the initial length. For this purpose, a longitudinal trabecula of the frog's auricle (stimulated by the sinus pacemaker) was used. The trabecula was isolated from the distal end. The experimental results demonstrated that with various loads optimal working effects could be obtained only with corresponding initial lengths of the trabecula. The latter proved incapable of even a slight working effort at the initial length with its distal end made free. Contraction of the trabecula with the minimal load becomes possible only after preliminary slight stretching.

With an increase in the load and the degree of stretching, the working effect of the trabeculae gradually rose to a maximal value and, having reached the limiting load, began to fall. The limit of stretching for one trabecula was 35%, and for the others 42-43.3% of the initial length. These degrees of stretching are limiting degrees on physiological grounds. With a further increase in the load, the trabeculae did not stretch any more and their working effect in these conditions fell sharply (see Fig. 3).

It may be considered from these experimental results that for the trabeculae to perform their optimal work the essential requirements are an average load and physiologically optimal degrees of stretching at rest. An excessive increase in the load was not accompanied by an increase in the length of the trabeculae over and above their physiological stretching. The strength of contraction did not increase further under these circumstances: on the contrary, the working effect fell rapidly.

A series of curves illustrating the working tension for a given constant initial length in relation to an increasing load (see Fig. 3), shows that the work of the trabeculae in these conditions begins to diminish much sooner, and falls gradually to zero as the load increases.

The curves of the first series (continuous lines) always lie at a higher level than those of the second series (broken lines) (see Fig. 3). This demonstrates that the performance of optimal (for these particular trabeculae) work during an increase in the load demands an increase in the initial, or "diastolic" length of the fibers as an essential condition. Only then can the maximal working effect be attained (stretching by 35.42 and 43.3%). This condition is also essential for maintenance of a high working tension at different levels of loading.

Our results are in agreement with those obtained by other workers [3, 4] experimenting on whole dogs' hearts, with multiple recording of the strength of the contractions of individual myocardial areas of the ventricle. Measure-

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
