

## TENSION AND SHORTENING VELOCITY OF RABBIT PAPILLARY MUSCLE UNDER INERTIA LOADING AT HIGH BEAT RATES

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### Abstract

Shortening and mechanical work were investigated in rabbit papillary muscle contracting under inertial loads at high beat rates. As long as the beat rates were below 100/min, an increase in rates always augmented the contraction under any inertial loads. The dynamic work for the muscle to exert motion to the inertia lever attained to the maximum at the equivalent mass of around 150 g and stayed nearly constant with further increase in the equivalent mass. At the beat rate of 150/min, the dynamic work showed the peak when the muscle contracted under the equivalent mass of about 150 g. Further increase in beat rates up to 200/min decreased the dynamic work under the given equivalent mass and reduced the value of the optimum equivalent mass under which the muscle performed the maximum dynamic work. The increase in beat rates showed the positive inotropic action on the mechanical work if the inertial loads were small, but under considerable amounts of inertia loading the inotropic action was turned to negative.

### INTRODUCTION

Since Bowditch described that the interval between contractions of heart was of importance in determining the strength of contraction, extensive investigations have been carried out on the inotropic phenomenon of beat rates not only in isolated cardiac muscles<sup>2,8,14)</sup> but also in isolated perfused hearts<sup>3,11)</sup> or in hearts *in situ*<sup>9)</sup>. The nature of this positive inotropic action was explained by the combined results of an increase in the degree of activation and of shortening of the active state. However, most of the previous studies in isolated heart muscles accounted for the tension as influenced by the beat rates but not shortening or velocity.

The present work was performed to study the shortening and the mechanical work under inertial loads at higher than physiological rates. The

results presented the optimum or the limit of the beat rate for the muscle to perform the maximum mechanical work.

### METHODS

The materials were the right ventricular papillary muscles of the albino rabbits. The experimental arrangements were the same as described in the previous paper<sup>10)</sup>. The muscle was connected with an ordinary isotonic lever which was combined to an inertia lever by a light chain. Therefore, the muscle encountered with inertial loads only in the acceleration phase of shortening. In the deceleration phase, the inertia lever departed from the isotonic lever and the muscle shortened under only static loads, preload and afterload. To avoid the oxygen deficiency in muscle during contraction at high rates, the resting periods for several minutes intervened between contractions lasting for 1 or 1.5 min. When the muscle repeated contraction and relaxation at high beat rate, an inertia lever was always moving up or down and was not kept at the balanced position. So, an electromagnetic stopper was placed to fix the lever and the muscle was subjected to contract in the isometric condition. Meanwhile, the inertia lever was controlled to be exactly balanced. After the positive inotropic action attained to the steady state, the stopper was quickly removed so that the muscle was allowed to shorten. The medium solution contained (mM) : NaCl 130, KCl 4, CaCl<sub>2</sub> 5, NaHCO<sub>3</sub> 10 and glucose 5.6, and pH was 7.2. The temperature of the solution was regulated at 32°C.

### RESULTS

#### 1. Force-velocity relationship in afterloaded contraction

The muscle was slightly stretched to about 0.9 of the length for the maximum isometric twitch tension. The force-velocity relationship in afterloaded contraction of the papillary muscle did not show the hyperbolic curves which Sonnenblick presented<sup>14)</sup>. Increase in beat rate from 60 to 100/min increased both tension and shortening velocity under a moderate load (about 1/3 of the isometric twitch tension). Namely, the inotropic action was positive. As the increase in beat rates to 150/min, however, the inotropic action for tension was converted into negative whereas the one for shortening was left positive. Further increase in rate to 200/min reduced tension, peak shortening and shortening velocity altogether. Although not directly determined, the maximum shortening velocity under zero load was expected to continue to be increased up to 200/min. In brief, tension or shortening of papillary muscle exhibited the separate inotropicism at the beat rates exceeding 150/min at 32°C.

#### 2. Peak shortening and shortening velocity under an inertial load

In Fig. 1, the procedures are shown for recording the contraction under

an inertial load at high beat rate. The muscle contracted at first in an isometric condition (Fig. 1, A). After the beginning of stimulation at the rate of 60/min, twitch tension increased gradually and attained to the steady amplitude in about 70 contractions. Meanwhile, the inertia lever was controlled to be exactly balanced. Then the muscle was allowed to shorten under the given equivalent mass (Fig. 1, E). Figure 2 shows the tension, shortening, shortening velocity and its square thus obtained at the beat rates of 100 and 200/min (afterload is 0.33g throughout). At the start of contraction, the active tension to impart the motion to the inertia lever was developed beyond the afterload, but it returned to the afterload level at the time of peak velocity or zero acceleration.

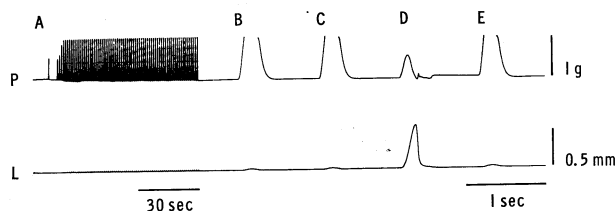


Fig. 1. Experimental procedures for recording the contractions under an inertial load. Beat rate is 60/min. At first, the electromagnetic stopper fixes the lever and the muscle contracts in an isometric condition (A, B, C). The stopper is quickly removed and the muscle is allowed to shorten under the equivalent mass of 154g (D). The stopper fixes the lever again and the muscle contracts isometrically (E).

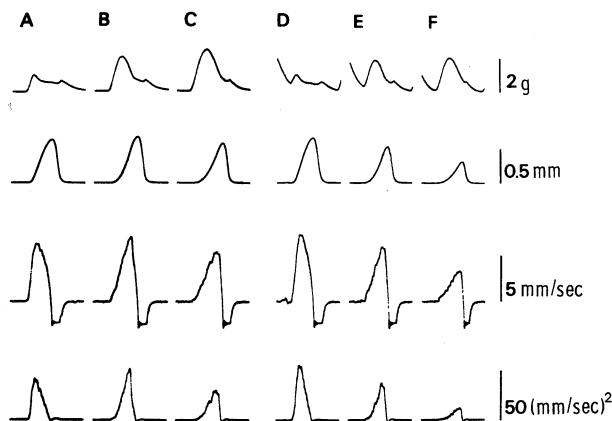


Fig. 2. Tension (top trace), shortening (second row), derivative of shortening (third row) and its square (bottom trace) under inertia loading. Beat rates, 100/min in A, B, C and 200/min in D, E, F. The equivalent mass is 10g in A, D, 80g in B, E and 154g in C, F. 32°C.

At the beat rate of 100/min, the velocity under the equivalent mass of 80g was higher than under 10g inertia. The result that the muscle shortened more rapidly under a certain inertial load than under zero inertia seemed to be unreasonable, but it was always observed even at low beat rates and was explained by the properties of the slow onset of the active state and of the deactivation caused by shortening<sup>6, 10, 12</sup>.

The peak and velocity of shortening with or without an inertia lever are plotted against the beat rates (Fig. 3). Under a small static load only, both peak and velocity of shortening increased with an increase in beat rates from 60 to 100/min and were kept nearly constant up to 200/min. Under a considerable amount of the equivalent mass (*e. g.* 154 g), the inotropic action for peak or velocity of shortening was positive below 100/min but it was negative above 100 or 120/min. These findings indicated that the increase in rates had two separate effects on contraction; one was to decrease the peak and velocity of shortening under large inertial loads and another was to increase them under small loads, and it was comparable to the results described in the previous section for the contraction under static loads.

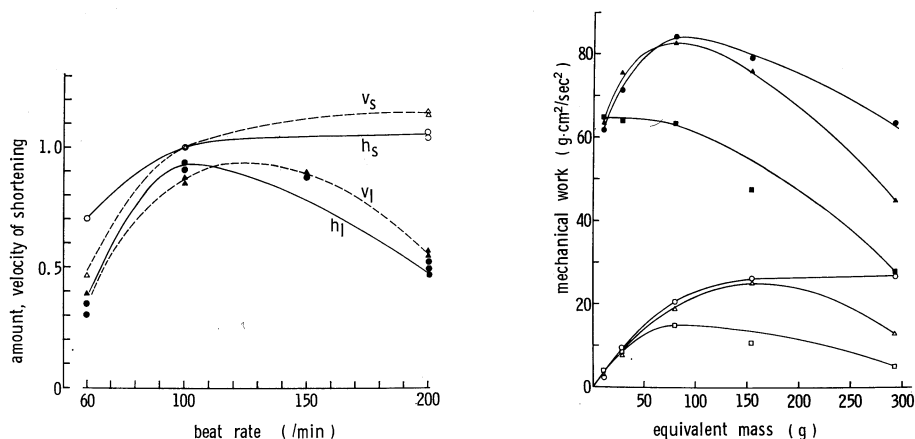


Fig. 3. Changes in peak shortening (circles and letters *h*) and velocity (triangles and letters *v*) at different beat rates. Hollow marks and letters *s* are the results from the contraction under 10g inertia load and filled marks and letters *l* are those under 154g, 32°C.

Fig. 4. Dynamic work (hollow marks) and total work (filled marks) against the equivalent mass. Circles are at the beat rate of 100/min, triangles at 150/min and squares at 200/min, 32°C.

### 3. Mechanical work done by muscle

The mechanical work ( $W$ ) done by muscle under inertia loading is described as,

$$W = m \cdot g \cdot h + \frac{1}{2} M \cdot v^2 \quad (1)$$

where  $m$  is a static load,  $h$  is a peak shortening,  $M$  is an equivalent mass of the inertia lever and  $v$  is a peak shortening velocity. The first term in eq. (1) means the static work and the second term the dynamic work. Figure 4 illustrates the dynamic work together with the total work done by muscle under different equivalent masses and at different beat rates.

At the beat rate of 100/min, the dynamic work was increased with an increase in the equivalent mass, attained to the maximum at 150g and was maintained constantly under large equivalent mass. The latter indicated that  $v$  decreased so as the product of  $M$  and  $v^2$  in eq. (1) to be constant. The muscle behaved as if it were a simple viscoelastic model. The total work decreased under the equivalent mass above 80g because of a decrease in peak shortening and a resulting decrease in static work.

At the beat rate of 150/min, the dynamic work was rather decreased under the equivalent mass of more than 150g. The velocity must be decreased much more than expected from the viscoelastic model. In these conditions, the muscle did no longer overcome an inertia loading. It is known as a peculiar property that a muscle mobilizes an extra energy depending on an applied load on it<sup>(4)</sup>. This property is conserved over a wide range of inertial loads if the muscle contracts at the rates less than 100/min. But, the muscle tends to lose this property if it contracts at the rates more than 150/min. As shown in Fig. 4, the maximum work at 200/min is decreased and the work attains to the maximum under the equivalent mass of about 80g, which is less than that is attainable at the beat rate of 150/min.

In summary, the increase in beat rates from 100 to 150/min shifts the optimum equivalent mass towards the smaller value, and further increase to 200/min reduces the maximum mechanical work accompanying a decrease in the optimum equivalent mass.

## DISCUSSION

Studies on the mechanical properties of the heart muscle has been extensively carried out, but most of them accounted for the contraction in isometric condition. The heart in the living body, however, contracts to eject the blood against not only the static load but also the dynamic load such as mass of blood and resistance in vessels. Brutsaert and others<sup>1,12,13</sup>, using the loading feedback circuit, investigated the contraction under the physiological loading and described that the dynamic load played an important role in resisting the contraction of the heart muscle. They also extended their study to explain the circulatory dynamics of the heart *in situ*. Our methods in the

present experiment, although they were simple, had advantages that they provided a large inertial load so as to reduce the mechanical parameters and also provided an inertial load so as to be applied on muscle only in the acceleration phase. The results also suggested that the roles of inertial loading was essential in considering the contraction of the papillary muscle when it was contracting at high rates.

The increase in the mechanical work with the increase in the inertial load indicated that the muscle exhibited the capacity to shorten by a given distance mobilizing an extra energy to overcome the resistance of an inertial load. The capacity of muscle, however, was not always maintained when the muscle was subjected to large inertial loads. Excess loading caused a decrease in the mechanical work especially in the dynamic work rather than in the static work. There should be a limit of the beat rate for the extra energy liberation. The limit was around 150/min, at which the optimum equivalent mass started to be shifted towards the smaller value. Recent paper of Ilebekk *et al.*<sup>5)</sup> showed the decrease in stroke volume of the heart *in situ* at high beat rate, independently of the initial muscle length.

There may be some questions in the methods of inertia loading. The inertia lever was simple and the equivalent mass was changed not finely but rather roughly. Secondly, the contraction under inertia loading was performed after a series of isometric twitches. Jewell and Rovell<sup>6)</sup> showed that peak and velocity of the shortening in the first isotonic twitch immediately after a series of isometric twitches were smaller than those in the steady isotonic twitches. Shortening and velocity measured in the present work may have been underestimated. The oxygen supply to the interior cells of the muscle preparation was also of importance, especially if the muscle contracted at high beat rates<sup>6)</sup>. In the present study, the sufficient resting periods were intervened between each record shown in Fig. 2, and the results were quite reversible,

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