Comparison of Contractile Performance of Canine Atrial and Ventricular Muscles

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ABSTRACT

This study compared the contractile performance of a canine right atrial trabecula with that of a macroscopically indistinguishable trabecula isolated from the right ventricular apex. The heart was removed from nine mongrel puppies weighing 6-8 kg and placed in Krebs-Ringer's bicarbonate solution. The bathing solution contained only 1.25 mmoles of Ca\(^{2+}\) and was bubbled with a 95% O\(_2\)-5% CO\(_2\) gas mixture. Each atrial trabecula was specially selected from the right atrial appendage. Histologically, these trabeculae showed a remarkable longitudinal orientation of the fibers. At L\(_{\text{max}}\) (the length of the muscle at which developed tension was maximum) under identical conditions of temperature, rate of stimulation, ionic milieu, pH, and O\(_2\) and CO\(_2\) supply, right atrial trabeculae achieved the same developed and total tensions but in a much shorter time than did ventricular trabeculae. In both muscle groups the maximum developed tension averaged about 2.5 g/mm\(^2\). Since L\(_0\) (expressed as a fraction of L\(_{\text{max}}\)) was less in atrial muscle than it was in ventricular muscle, we concluded that atrial muscle can be stretched considerably more than can ventricular muscle before optimum length is reached. At any given initial muscle length, the maximum of tension rise for atrial trabeculae amounted to at least twice that for ventricular trabeculae. At any given load up to 1.5 g/mm\(^2\), the maximum velocity of shortening of an atrial trabecula was about three to four times that of a ventricular trabecula. These results collectively indicate that the contractile performance of the right atrial muscle is in many respects superior to that of the right ventricle, at least under the conditions of these experiments.

The present study was conducted to compare the contractile performance of a canine right atrial trabecula with that of its right ventricular counterpart under identical experimental conditions.

Methods

Nine mongrel puppies of either sex (12 ± 4 weeks of age, 6-8 kg) were anesthetized with sodium pentobarbital (30 mg/kg, iv). The entire heart was then rapidly removed and placed in a beaker of Krebs-Ringer's bicarbonate solution that was being bubbled at 37°C with a 95% O\(_2\)-5% CO\(_2\) gas mixture. The bathing solution contained (mmoles/liter): Na\(^+\) 145, K\(^+\) 4.2, Ca\(^{2+}\) 1.25, Mg\(^{2+}\) 1.2, Cl\(^-\) 125, SO\(_4\)\(^{2-}\) 2.4, H\(_2\)PO\(_4\)\(^-\) 1.2, HCO\(_3\)\(^-\) 25, and glucose 5.6. The same continuously oxygenated and stirred solution was also utilized for isolated muscle perfusion. After equilibration, the solution had an oxygen tension (P\(_{O2}\)) of 550 mm Hg or greater and a pH of 7.40 ± 0.02.

Ventricular trabeculae were all removed from the apical region of the right ventricle, and each trabecula was obtained from the right atrial appendage. We have found that certain trabeculae of the right atrial appendage are not randomly distributed (unpublished observation). In the present study we chose the trabecula coursing from the crista terminalis adjacent to the sinus node toward the vortex of the right atrial appendage (Fig. 1). Histologically, these trabeculae showed a regular longitudinal orientation of the fibers (Fig. 2). In these histological sections, atrial trabeculae did not appear to have more interstitial connective tissue nor were they surrounded by a greater amount of endocardium than were ventricular trabeculae.

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The muscles were mounted in an experimental apparatus that has been described previously (20, 25, 26). One end of the muscle was attached to a fixed force gauge with no measurable nonlinearity in the tension signal over applied forces up to 10 g. The other end of the muscle was attached to a light aluminum pendulum for determination of length changes. Positional changes of the length lever were sensed by a linear differential transformer whose small iron core was firmly attached to the lever. The equivalent mass of the lever was 0.3 g, the length lever were sensed by a linear differential determination of length changes. Positional changes of the lever movement, was used to set the muscle lengths.

Atrial appendage. The open arrow indicates the anchorage of the superior vena cava. Opening the right atrium along the crista terminalis (CT) and the atrioventricular sulcus (AVS) exposes the entrance to the atrial appendage. The open arrow indicates the anchorage of the crista terminalis and the white arrow identifies the right atrial trabecula utilized in this study. SN = sinus node and SVC = superior vena cava.

Figure 1

Opening the right atrium along the crista terminalis (CT) and the atrioventricular sulcus (AVS) exposes the entrance to the atrial appendage. The open arrow indicates the anchorage of the crista terminalis and the white arrow identifies the right atrial trabecula utilized in this study. SN = sinus node and SVC = superior vena cava.

Results

SELECTION OF AN APPROPRIATE TEMPERATURE AND STIMULATION RATE

In most species a change in temperature profoundly influences both the membrane potential and the myocardial contractile performance. Temperature affects contractile performance in both atrial and ventricular trabeculae. Pilot experiments conducted to select a temperature and a rate of stimulation at which both the atrial and the ventricular muscles would perform optimally for at least 24 hours showed that a temperature of 25°C and a stimulation rate of 12 beats/min satisfied these requirements (Fig. 3).

COMPARATIVE LENGTH-TENSION DIAGRAMS

In five atrial and four ventricular trabeculae, isometric beats were obtained and analyzed at twelve different initial muscle lengths. Figure 4 is the composite graph obtained after the means of their respective resting and developed tensions measured at four selected initial muscle lengths were plotted. Four points were chosen for comparative purposes because only these points were exactly common to each muscle of each group. Discrimination between loads varying from 0 to 50 mg was difficult and often unreliable. For this reason,
in the present study, $L_o$ of atrial and ventricular trabeculae was arbitrarily defined as the muscle length at which the average preload was equal to 70 ± 20 mg.

In the five atrial trabeculae, $L_o$ averaged 0.866 mm/$L_{\text{max}}$. The relationship between the resting or the developed tensions and the corresponding initial muscle lengths was well estimated by a straight line. In the four ventricular trabeculae, $L_o$ averaged 0.920 mm/$L_{\text{max}}$. The relationship between the resting or the developed tensions and the corresponding initial muscle lengths was approximately a straight line. $L_o$, expressed as a fraction of $L_{\text{max}}$, was less in atrial muscle than it was in ventricular muscle ($P < 0.05$). Atrial muscle can thus be stretched considerably more than can ventricular muscle before optimum length is reached. At $L_o$, atrial and ventricular muscles developed almost the same tensions. This was also the case at $L_{\text{max}}$ where the developed tension of atrial muscle was $2.43 \pm 0.46$ g/mm² and that of ventricular muscle was $2.63 \pm 0.52$ g/mm². At $L_{\text{max}}$, the resting
Records illustrating the effect of three different temperatures on the contraction of a canine right atrial and right ventricular trabecula. Both muscles were studied at L\textsubscript{max} and stimulated 12 times/min. Note that tension is inscribed from bottom to top, whereas shortening expressed as a fraction of L\textsubscript{max} is inscribed from top to bottom. At 25°C both muscles generated a tension amounting to approximately 2.5 g/mm\textsuperscript{2}.

Tensions were also similar, being 0.53 ± 0.12 g/mm\textsuperscript{2} in atrial muscle and 0.43 ± 0.17 g/mm\textsuperscript{2} in ventricular muscle.

Table 1 summarizes our data collected at L\textsubscript{max} with a comparative statistical evaluation of the means obtained. These results indicate that at L\textsubscript{max} the cross-sectional area, weight, muscle length, resting tension, and developed tension were not significantly different. In contrast, all measurements of duration were significantly different (P < 0.01). For example, the latency period in the atrial trabeculae was briefer and averaged only 66% of that in the ventricular trabeculae. Other measurements of duration in the atrial muscles ranged between 50% and 76% of the corresponding measurements in the ventricular muscles.

Changes in maximum rate of tension rise as a function of length

Figure 5 shows measurements obtained in both atrial and ventricular muscles and illustrates the characteristic succession of changes in the maximum rate of tension rise as a function of length. Again a straight line was chosen to express this relationship. This diagram also indicates that at any given initial muscle length the absolute values for maximum rate of tension rise achieved by atrial
trabeculae were significantly greater ($P < 0.05$) than those developed by ventricular trabeculae.

**CHANGES IN TIME TO MAXIMUM TENSION AS A FUNCTION OF LENGTH**

Figure 6 represents changes in time to peak tension as a function of initial muscle length. The relationship is expressed as a straight line. Changes in initial muscle length had no significant influence on atrial time to peak tension, whereas comparable changes in initial muscle length significantly affected time to peak tension in the ventricle. This latter effect, however, was at best moderate, since the difference was only significant ($P < 0.05$) when the mean of the time to peak tension measured at $L_o$ was compared with the mean of the time to peak tension measured at $L_{max}$.

**CHANGES IN DURATION OF CONTRACTION AND IN RELAXATION TIME AS A FUNCTION OF LENGTH**

In both tissues the duration of the contraction progressively increased with increments in initial muscle length. Figure 7 is the graphic display of this relationship. At any given initial muscle length, the duration of an atrial contraction was significantly briefer ($P < 0.01$) than the duration of a ventricular contraction. Any given increment in

![Figure 5](image_url)

*Figure 5. The progressive increase in the maximum rate of tension rise as a function of initial muscle length, compared in canine atrial and ventricular trabeculae. At $L_{max}$, the mean rate of tension rise in atrial trabeculae was more than twice that observed in ventricular trabeculae.*

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**TABLE 1**

| Values from the Length-Tension Curves Obtained in Canine Right Atrial Trabecula and Four Canine Right Ventricle Trabeculae at $L_{max}$ |
|---|---|---|---|---|
| Cross-sectional area | Length | Weight | Resting tension | DVP | MTRT | TMXT | TLAT | TRN |
| Atrial-trabeculae | 5.78 ± 1.13 | 5.24 ± 0.87 | 1.11 ± 0.35 | 0.52 ± 0.19 | 2.49 ± 0.43 | 2.48 ± 0.88 | 1.11 ± 0.08 | 0.62 ± 0.08 |
| Ventricle-trabeculae | 6.86 ± 2.56 | 6.54 ± 0.96 | 1.11 ± 0.22 | 0.33 ± 0.11 | 2.59 ± 0.13 | 2.03 ± 0.38 | 1.93 ± 0.07 | 0.06 ± 0.01 |
| Rate: 12 Beats/Minute **Temp: 25°C** | **Duration of contraction** | **Latency time** | **Rate of tension rise** | **Recovery time** | **Maximum rate of tension rise** |
| Atrium | $y = -17 + 98x$ | $r = 0.92$ | **Ventricle** | $y = -47 + 56x$ | $r = 0.71$ | **Maximum Rate of Tension Rise in kPa/cm²** | **Length in mm/L_{max}** |
| Rate: 12 Beats/Minute **Temp: 25°C** | **Latency time** | **Rate of tension rise** | **Recovery time** | **Maximum rate of tension rise** | **Length in mm/L_{max}** |

*All values are means ± s.d. DVP = maximum developed tension, MTRT = time to maximum rate of tension rise, TMXT = duration of contraction, TRN = latency time, TLAT = rate to maximum rate of tension rise from duration of contraction, NS = not significant ($P > 0.05$).*
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Changes in time to peak tension as a function of initial muscle length compared in canine atrial and ventricular trabeculae. In the ventricle, changes in initial muscle length from 94% of L\textsubscript{max} up to L\textsubscript{max} barely influenced the time to peak tension.

initial muscle length resulted in a corresponding proportional change in the duration of either an atrial or a ventricular contraction, but the latter always required a longer time. Similarly, relaxation time increased with increments in initial muscle length in both types of muscle, but at any given initial muscle length relaxation time was significantly shorter (P < 0.01) in the atrium.

ISOTONIC SERIES

Table 2 summarizes force–muscle shortening relationships obtained at L\textsubscript{max} with a constant afterload of 1 g. L\textsubscript{max} was chosen because at this length both muscle specimens had similar resting, developed, and total tensions. Table 2 also shows a statistical evaluation of the differences between the respective means. Cross-sectional area, weight, and length are the same as those cited in Table 1. Under these experimental conditions, there was no significant difference between the resting tension of atrial and ventricular trabeculae. (There was also no detectable difference between resting tension of atrial and ventricular trabeculae when they were studied under isometric conditions.) The distance shortened and the maximum velocity of shortening were both significantly greater (P < 0.01) in the atrium than they were in the ventricle. The latency period, the time to maximum velocity, and the time to maximum shortening were all significantly briefer (P < 0.01) in the atrial tissue.

SHORTENING AS A FUNCTION OF LOAD

Both atrial and ventricular muscles at L\textsubscript{max} developed a comparable tension which averaged approximately 2.5 g/mm². From fifteen different routine afterloaded contractions, three representative examples of these loads were selected for comparative purposes. Figure 8 illustrates a progressive decrease in shortening with increments in load. At loads of 1 g and less, any increment in load resulted in a greater decrease in shortening in the atrium than it did in the ventricle (P < 0.01). For loads of 1.5 g or more, there was no significant difference between the amount of shortening achieved by the two specimens.

VELOCITY OF SHORTENING AS A FUNCTION OF LOAD

At L\textsubscript{max} any increment in load decreased the velocity of shortening more in the atrial muscle than in the ventricle.
TABLE 2

<table>
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<tr>
<th></th>
<th>Weight</th>
<th>Length</th>
<th>Cross-sectional area</th>
<th>Resting tension</th>
<th>DLTL</th>
<th>MAXV</th>
<th>TLAT</th>
<th>TMXV</th>
<th>TMXS</th>
<th>DRTN</th>
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<tr>
<td>Atrial trabeculae</td>
<td>5.78 ± 1.13</td>
<td>5.34 ± 0.87</td>
<td>1.11 ± 0.26</td>
<td>0.503 ± 0.122</td>
<td>0.069 ± 0.010</td>
<td>0.613 ± 0.085</td>
<td>52.0 ± 9.1</td>
<td>156.0 ± 10.9</td>
<td>273.4 ± 23.8</td>
<td>604.0 ± 37.7</td>
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<tr>
<td>Ventricular trabeculae</td>
<td>6.85 ± 2.73</td>
<td>5.95 ± 0.96</td>
<td>1.11 ± 0.32</td>
<td>0.424 ± 0.197</td>
<td>0.0405 ± 0.0104</td>
<td>0.181 ± 0.0033</td>
<td>78.8 ± 13.6</td>
<td>275.3 ± 29.7</td>
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</tr>
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</table>

All values are means ± s.d. DLTL = maximum muscle shortening, MAXV = maximum velocity of shortening, TMXV = time to maximum velocity of shortening, and TMXS = time to maximum shortening. NS = not significant (P > 0.05).

Progressive decrease in shortening (ΔL) as a function of load

Extrapolation of the straight lines gave y-intercept: 0.12

Figure 8

Shortening (ΔL) in mm/Lmax

Load in g/mm²

Rate: 12 Beats/Minute

Temp: 29°C

Comparison between time to maximum velocity of shortening and time to maximum rate of tension rise

Figure 11 illustrates the progressive increase in time to maximum velocity with increasing load. At all loads studied, atrial trabeculae reached maximum velocity in a significantly shorter period of time (P < 0.01) than did ventricular trabeculae. When the load approached 20% of the peak developed isometric tension, shortening of an atrial trabecula was almost twice that observed in a ventricular trabecula.

The relationships were estimated by straight lines. Extrapolation of the straight lines gave y-intercept: 0.14
At 12 Beats/Minute
Temp: 25°C

FIGURE 9
Progressive decrease in maximum velocity of shortening as a function of load compared in canine atrial and ventricular trabeculae at $L_{\text{max}}$. At low loads, the velocity of shortening of an atrial trabecula was about four times that of a ventricular trabecula.

Atrium
\[ y = 1.03 - 0.40x \]
\[ r = 0.83 \]

Ventricle
\[ y = 0.29 - 0.11x \]
\[ r = 0.81 \]

Load in g/mm²

Velocity of Shortening in mm/sec

FIGURE 10
Comparison between the force-velocity curves of canine right atrial and right ventricular trabeculae at $L_{\text{max}}$. Linear extrapolations (dotted lines) demonstrate that $V_{\text{max}}$ in the atrial trabecula was about four times that in its ventricular counterpart.

Discussion
One well-known property of atria is their distensibility. In fact, recent investigations in the frog have shown that sarcomere lengths up to 3.5 μm can readily be obtained when an appropriate stretch is applied to atrial trabeculae (24, 28, 29). We can now consider whether canine atria have comparable sarcomere properties. The present study demonstrates that canine right ventricular muscle clearly offers far greater resistance to stretch than does canine right atrial muscle, since at $L_{\text{max}}$ the former has undergone only about two-thirds of the elongation of the latter.

One of the most distinctive features of the contractile performance of right atrial trabeculae was that they achieved the same developed and total tensions in a much shorter time than did ventricular trabeculae. One might speculate that the slower development of tension characteristic of the contraction of a ventricular trabecula is due to a different anatomical arrangement of the myofibers. However, it also could reflect a functional difference, such as a faster rate of appearance of active sites in atrial trabeculae. In both muscle
groups, the maximum developed tension averaged approximately 2.5 g/mm². This relatively low developed tension was due to the fact that we chose a lower concentration of calcium than that used in previous study (26). However, the 1.25 mmol/liter of calcium utilized in the present study closely corresponds to the ionized calcium fraction of canine and human blood. The amount of developed tension observed was about half that measured in cats by utilizing 2.50 mmol/liter of calcium (26).

Although the amount of shortening accomplished by atrial muscle at any given load in excess of 1.5 g/mm² was not significantly different from the shortening measured in the ventricular muscle, at any load the time to maximum shortening was significantly briefer in the atrium. At any given initial muscle length, the maximum rate of tension rise in the atrium amounted to at least twice the value measured in the ventricle. At any given load from 0.5 to 1.5 g/mm², the maximum velocity of shortening was significantly greater in the atrium, and V\text{max} of an atrial trabecula was about four times that of a ventricular trabecula. These results collectively indicate that the contractile performance of a right atrial muscle from the appendage is in many respects superior to that of a right ventricular apical trabecula.

It is possible that some of the differences between atrial and ventricular muscle found in this study, such as the greater velocities and briefer durations in the atrial muscle, are due to the greater concentration of norepinephrine normally found in atrial muscle (30). This difference, however, cannot account for the differences noted in the amount of stretch required to reach L\text{max}. It should also be noted that, since the present study used only young dogs, it is possible that some or all of the observed differences are due simply to differences in the maturation rate between the atrium and the ventricle. Developed force (31) and maximum velocity of shortening (32) do increase with age in certain mammalian species.

Since under normal conditions atrial contractions not only precede but ideally should be completed by the time of onset of ventricular contractions, one would teleologically reason that the time course of atrial mechanical events must be of brief duration. But the magnitude of shortening and the amount of tension developed by our atrial trabeculae are such that one of the most obvious questions from this study is whether the right atrial appendage is really only a contractile appendix or has some other important physiological function yet to be defined.

References

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