Structural basis for cardiac function

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MATERIALS AND METHODS

A total of 42 hearts from nine different mammalian species: ground squirrel (5), marmot (4), elk (1), cat (2) dog (20), baboon (3), human (4), cow (2), and elephant (1), were examined as follows:

Anatomical

Atrial tissues and major vessels were removed and cross-sectional dimensions analyzed. The majority of hearts studied were in a diastolic state; however, a few were analyzed in a fully contracted state to note the difference in gross dimensions and in fiber orientation.

As employed in this study, a strand of fibers denotes an elongated muscular structure that can be visibly differentiated from surrounding myocardial tissue, thus allowing one to judge the plane and direction of its major axis. The direction of the superficial strands was determined by stripping off the outer connective tissue, and the primary direction furnished a zero base line from which deeper fiber orientation was measured. Fresh hearts were used in all species except for specimens from the elk and the baboon which were preserved in formalin.

The base of each heart was carefully dissected to delineate the fibrous tissue organization frequently referred to as the cardiac skeleton. A fiber strand analysis was then carried through the depths of both ventricles to determine changing orientations at fixed distances from the epicardial surface. The muscular strands rotated through a considerable angular change immediately beneath the epicardium, and then for a majority of myocardial thickness, little angular change was noted (Figs. 2 and 3) until the endocardium was reached. The minimally changing fiber orientation of the ventricular bulk is referred to as the principal fiber direction.

Cross-sectional (vertical and horizontal) analysis of hearts stopped in systole or diastole and the radii of curvature at different anatomical regions of the ventricles were measured in an attempt to differentiate inflow and outflow tracts in 10 canine right ventricles.

Two dog hearts were arrested and allowed to dilate while two others were arrested in a maximal systolic state under the influence of calcium citrate. An outer mold of plaster of paris prevented distension and both chambers of these hearts were filled with plaster of paris to create a mold of the ventricular cavities. In left ventricular casts the volume of papillary muscle was measured and related to cast volume; the configuration of these casts was analyzed.
Finally, the wet weights of papillary muscles freshly removed from 10 canine hearts were measured to compare the relative bulk of the two muscles.

Functional

The chests of four dogs (18–22 kg), under phencyclidine hydrochloride (2 mg/kg im) and α-chloralose (60–80 mg/kg iv) anesthesia and positive-pressure respiration, were opened and hearts exposed. Four modified Walton-Brodie strain gauges were sutured to the epicardial surface of the right ventricle, the sutures being superficially placed so that the underlying muscle was taut (19); an increase in tension of the muscle segment between the feet was recorded as an upward deflection on a Grass polygraph and Tectronics four-channel oscilloscope.

The longitudinal orientation of the gauges was altered on the sinus and conus of the right ventricle to monitor normal contraction (Fig. 9, left panel), and a ventriculotomy of approximately 90% of the wall thickness was performed between the gauge feet. The depth of ventriculotomies was confirmed upon autopsy. The gauges were placed parallel to the major fiber strand orientation or at right angles to that axis in order to ascertain the importance of such orientation. When the integrity of fiber strands was interrupted by the ventriculotomy so that the incision gaped, the gauges recorded a negative deflection in all four experiments.

RESULTS

Anatomical

Except for gross dimensional differences, ventricular fiber orientation was similar in all hearts. The uniformity of fiber orientation in mammalian hearts may be categorized into three parts: A) the cardiac skeleton, B) the left ventricle, and C) the right ventricle.

A) Cardiac skeleton. The fibrous structures at the base of the heart from which muscle fibers both take origin and insertion consist of four triangular shaped local accumulations of tough fibrous tissue interconnected by a thin fibrous band, which also sprouts out around the mitral and tricuspid orifices. These four triangles are located as follows: right anterior, left anterior, right posterior, and left posterior (Fig. 1, upper left, no. 2, 1, 3 and 4). From the right anterior triangle arise the strands that surround the right ventricular conus (Fig. 6). The right lateral cusp of the aortic valve overrides the interventricular septum and aids in formation of the right anterior and right posterior triangular fibrous regions. Extending from the base of the skeleton is a cylinder (about 1 cm deep in canine hearts) of fibrous tissue from which originate the deeper fibers of the left ventricle (Fig. 1, fiber origin) to form a strong cuff around the aortic orifice.

B) Left ventricle. The superficial strands of the left ventricle descend in a nearly vertical direction from the plane of the aortic orifice to apex on the anterior and posterior surfaces of the heart (Figs. 1 and 2); this is more evident during diastole, for in systole these fibers tend to twist laterally and assume a more horizontal position. The septal fibers (visualized by removal of the right ventricular trabeculae) are also predominantly vertical in the outer layers. Approaching the left lateral border of the left ventricle and mitral ring, the outer fibers become obliquely directed (Fig. 1). The superficial fibers at the apex whirl clockwise (when viewed from the apex) into a tight helix (Fig. 2).

It is the deeper ventricular strands that have given rise to much confusion. To facilitate understanding, these will be separated into two groups: 1) the bulk of the fibers which encircle the ventricle, and 2) the endocardial fibers, trabeculae carneae, and papillary muscles.

**FIG. 1.** Base of left ventricle with atrium and right ventricle removed is illustrated. Points 1 and 4 represent fibrous triangles (left anterior and posterior) at junction of aorta and mitral valves (upper insert). Between right triangles (no. 2 and no. 3) is base for right cusp of aortic valve, overriding septal region. Right lower insert illustrates fibrous raphe which hangs from aortic root, and from which a great bulk of muscle strands originate. Note fiber strand directions around mitral orifice.

**FIG. 2.** Outer fibrous layer and right ventricle have been removed. Anterior portion of heart is illustrated, with septal wall above and to left of cut. Orientation of epicardial fiber strands is clearly visible, as is apical ventricle. Upon dissecting endocardially, an angular direction change of strands is evident; it will be noted that just before strands undergo a rapid change, majority of them are relatively parallel—principle fiber direction. Deep in region a rapid transition to near vertical strands is depicted endocardial-papillary muscle portion of musculature.
l) The bulk of the deep strands undergo nearly 90° angular change in orientation (Figs. 2 and 3). Dissecting endocardial from the epicardium, the fiber strands change direction from the vertical to a position at right angles to the vertical just before reaching the endocardium (Fig. 2). Vertical epicardial strands at the base descend only a short distance before penetrating deeply while rotating toward a horizontal subendocardial position. Such strands make up the bulk of the left ventricular mass with some regional variation (Fig. 3). The anterior (Fig. 3, no. 3), septal (Fig. 3, no. 2), and posterior muscle regions show a fairly uniform right angular directional change from epicardium through to the endocardium, the principle fiber direction of the major muscle mass twisting at an angle 50°-60° relative to the vertical axis, as is demonstrated in Fig. 2. The septal wall is continuous with fiber strands of the left ventricle; proceeding from the right ventricular endocardial surface of the septum toward the left ventricular endocardium, the muscle strands undergo directional changes comparable to those described for the anterior left ventricle (Fig. 3, no. 2). In smaller hearts the major fiber direction is easily followed as major strand orientations change in a short distance. In systole, the mitral orifice is reduced in diameter, and the principle fiber direction of the circummitral strands becomes nearly horizontal. The apical region forms a verticil (Fig. 2) arising from epicardial fibers which rotate obliquely then swing in a clockwise direction (when viewed from the apex) to plunge into the ventricular wall. The outer fibers of the left ventricle plunge apically into the left ventricular papillary muscles, thus forming the vertical, parallel muscle strands which characterize these structures (Fig. 3, insert 3).

2) A major fraction of the trabeculae carneae, papillary muscles, and endocardial fibers are made up of vertically oriented fibers (except for lateral running trabeculae). Thus, from the deep fiber strands which characterize the bulk of the ventricle (Fig. 2), there is a rapid change in fiber orientation (i.e., 90° in 1 or 2 mm of depth) to form the vertically oriented endocardial fibers (Fig. 3, insert 2). On horizontal cross section of the ventricle, this region of acute change in fiber orientation clearly delineates the muscle bulk from the endocardial fibers (Fig. 4). When one considers vertical and horizontal cross sections (Fig. 4), gross enlargement of papillary muscle cross section has a great influence on cavity geometry, a phenomenon which is not generally appreciated. Because of the relative increase in volume displacement by the papillary muscles during systole, the inframitral region is filled and a smooth outflow tract to the aortic orifice becomes prominent (Fig. 4, vertical cross section) as is clearly visualized in plaster molds of the canine ventricular cavity in systole and diastole (Fig. 5). The papillary muscles in diastole are relatively small and delineate a large submitral inflow region, the bulk of the diastolic cast consisting primarily of this inframitral volume tract (Fig. 5). The papillary muscle volume in relation to total chamber volume in two diastolic casts averaged 8%. The casts during calcium-arrested systolic state (Fig. 5, right side) with comparatively small total volume show a large indentation (P) where the papillary muscles protrude (30% of the chamber volume). On cross section (Fig. 4) they close off this region and

![Diagram](http://ajplegacy.physiology.org/Downloadedfrom/10.1152/jappl.1977.25.10.1519)

**Fig. 3.** Schematic representation of 4 regional muscular strand orientations, as seen by incision in Fig. 2. Fans demonstrate angular change that fibers undergo in each identified region; lowest nearly vertical arm of fan represents orientation of epicardial fibers, their angular change (in degrees), and thickness of muscle (mm) in which this change occurs. Section accentuated by miniature fans comprises bulk of muscle; both thickness and angular change are again recorded. It is this region which demonstrates direction which most of strands follow—principle fiber direction. Last sector of fan, only present in recordable mass in areas 2 and 3, represents endocardial fibers, trabecular and papillary muscles (insert 3), strands rotate rapidly 90° and then make up bulky papillary muscle. Insert 2 represents intraventricular septum with right ventricular trabecular muscle removed.

![Diagram](http://ajplegacy.physiology.org/Downloadedfrom/10.1152/jappl.1977.25.10.1519)

**Fig. 4.** Cross-sectional dimensions of left ventricle in diastole (left) and systole (right) illustrate variations of internal configuration caused by papillary muscles. In diastole papillary muscles protrude minimally, cavity being relatively globular. In systole papillary muscles, especially anterior papillary muscle, bulge into cavity leaving a smooth walled infra-aortic outflow tract. Region of rapid fiber-strand transition noted in Figs. 2 and 3 is shown by dashed line.
accentuate the cylindrical outflow channel up to the aortic root—the outflow tract (Figs. 4 and 5). Trabeculation of the dog ventricle is minimal, having little prominence in either cross-sectional views or plaster casts.

The average weights of the papillary muscles, severed flush from the right and left ventricles, of 10 canine hearts are given in Table 1. Total ventricular weights (both right and left) are related to whole-animal weights. The right ventricular mass was carefully isolated, leaving the interventricular septum as an integral part of the left ventricle. The papillary muscles from both chambers were blotted dry and weighed. The muscles in the left ventricle were grossly identified as anterior and posterior, while those from the right ventricle were grouped and weighed together. The anterior muscle of the left ventricle was consistently approximately double the weight of the posterior.

Anatomically and embryologically the right ventricle is divided into two regions: 1) The inflow (sinus) and 2) the outflow (conus) regions.

1) Inflow region. The fibers of the bulk of the right ventricle are oriented like those in the left ventricle. They originate from the posterior skeletal triangle (Fig. 1, no. 3) and swing around the tricuspid orifice (Fig. 6). The fibers rotate through approximately 160° from epicardium to endocardium (Fig. 7). A principal fiber direction also exists in the right ventricle, again being oblique (to the base to apex vertical) in direction (Fig. 7, no. 1). Fibers of the endocardium do not change orientation as much as on the left side (approximately 50°). The apical region consists of fibers blending with the septal fibers; in some hearts (cow) this region is very thin (10% of the basal thickness), whereas in others (human), it is relatively thick. No secondary helix was found in the right ventricle.

The human right ventricle is heavily trabeculated, and at the origin of the outflow tract a papillary muscle-trabeculae complex, the crista supraventricularis (2), sometimes exists. This structure is very prominent in the eland heart.

2) Outflow tract. The outflow tract of the right ventricle has a peculiar embryologic development arising from the circumvascular fibers (as is found in species such as the turtle). The fibers of this region are primarily circumcaval in direction (Figs. 6 and 7, no. 3).

Fiber strands originate from the right anterior skeletal triangle and swing around the conus (Fig. 6) to emerge near their origin and blend with the apically directed fibers of the anterior left ventricle. Sometimes the anterior descending coronary vessel courses beneath these fibers. Although there is a collection of fibrous tissue in the conal region, no conal "ligamentous" attachment to the cardiac skeleton was noted. The conal strands undergo only minimal (10°) angular rotation exclusive of endocardial fibers and are parallel in their circumcaval course (Fig. 6 and Fig. 7, no. 3). There is gradual blending with the sinal fibers; in some species, the majority of conal fibers are parallel from epicardium to endocardium, whereas in others (human), there is as much as 20° angular rotation. The
endocardial strands are oriented at right angles to those of the epicardium, and this alteration of direction (approximately 80°) occurs very rapidly. In the dog the endocardial layer is so thin, it is difficult to detect; however, with the prominent trabeculations in man, it is much more evident. In the cow, it occupies 5% of the total conal thickness.

Cross sections of the inflow and outflow regions of the right ventricle were made in canine hearts (Fig. 7). The radius of curvature of the inflow region was found to be from 40 to 52 mm, while that of the outflow region was from 8 to 10 mm, a 5:1 ratio. Plaster casting of the right ventricle in systole revealed a distinct separation of the cavity at the junction of the inflow (labeled S in Fig. 8) and outflow (labeled C in Fig. 8) regions; this delineated the region of transition from conal to sinus fiber orientation, the location of a systolic groove sometimes noted in vivo. Diastolic casts of the right ventricle failed to reveal such a region of stricture.

Functional Studies

Ventrilotomy incisions were made through 90% of the myocardial thickness of the right ventricle in the midsinus and conus regions (Fig. 9). The orientation of these incisions was a) parallel, or b) at right angles to the principal fiber direction. Strain gauges were placed in such a manner as to reveal whether ventrilotomy disturbed function; the integrity of the region was altered when the incision gaped during systole. The right ventricular incisions had striking effects on muscular function.

Ventriculotomy did not grossly alter the integrity of muscular contraction in the inflow (sinus) region no matter what its direction (Fig. 9, no. 4); the recorded peak force was reduced to 75 ± 5% of control after the incision. Also, when the incision was made circumonally, that is, parallel to the fiber strand orientation of the outflow tract, no gross alterations in contractile force were noted. In the four experiments the peak force was reduced minimally (85 ± 2% of control). However, when incisions were performed at right angles to the primary direction of conal fibers (Fig. 9, no. 2), gross alterations occurred. Although paraventriculotomy gauges still recorded positive deflections (Fig. 9, no. 1 and no. 3) showing that the incision did not cause gross contraction alteration in surrounding muscle, the gauge straddling the incision showed inversion of primary waves (Fig. 9, no. 2). The inverted force trace was, when compared to control force traces, −72 ± 15% of control. With muscle fibers cut and the circumoncal integrity destroyed, the region did not have the capacity to close the incision. This is in sharp contrast to the pre-incisional function (Fig. 9, left panel) as well as the effect of sinus region incisions (Fig. 9, no. 4).

DISCUSSION

The utilization of fresh specimens did not substantiate conventional concepts of cardiac architecture as consisting
of “scrolls of muscle bands” composed of discrete superficial and deep bulbspiral and sinospiral muscles. Earlier workers (1, 11, 31), relating function and embryology to structure, considered ventricular muscle to be a continuous network (11, 12), the direction of fibers being of physiological significance. However, despite a number of anatomic evaluations (6, 9, 13, 20, 23, 27, 28, 30), a simplified anatomical picture necessary to develop myocardial mechanics (5, 6) has not evolved.

The present structure-function analysis stresses three basic characteristics. 1) The ventricle is made up of a continuum of interdigitulating fibers which do not sharply delineate into separate muscular bands. 2) Deep fibers are oriented at right angles to epicardial fibers, a transition of angular change occurring between them (Fig. 2). There is a “principal fiber direction” consisting of the bulk of ventricular fibers which is generally oblique to a vertical base to apex axis (Fig. 3). 3) Epicardial fibers originate from the aortic root arcus, descend, and at the apex enter deeply to form a major part of the papillary muscles reinserting into the mitral ring via the chordae tendineae. However, a significant portion of muscle strands do not pass from base to apex but swing deeply from epicardium toward the endocardium at all vertical levels.

The cardiac skeleton (15) consists of four interconnected triangular fibrous regions around the aortic base (Fig. 1, upper inset). A fibrous raphé hangs from this annulus fibrosus, extending towards the apex (Fig. 1, lower inset) and serves as both origin and insertion of the muscle mass. The superficial fibers extend from the upper part of the infra-aortic cylinder vertically to the apex or obliquely around the mitral orifice, and the deeper fibers from the lower portion of this cylinder form the bulk of the obliquely running muscle fibers—the principle fiber direction (Fig. 1, lower inset). The principle fiber direction in any region of the myocardium presumably determines the major direction of contraction, thus primarily reducing the oblique and circumferential dimensions (8, 24). The outer fibers swirl at the apex and plunge to the inside, forming a large portion of the vertically-oriented papillary muscles reinserting into the mitral region via the chordae tendineae; this continuum of fiber direction is evident early in embryologic development (29). More fibers enter the anterior papillary muscle making it about twice the weight of the posterior papillary muscle (Table 1).

An important function of the papillary muscles is ascribed to their formation of an inflow tract in diastole (Fig. 4) (14); in systole these muscles increase in cross-sectional diameter to fill in the inflow tract (9, 25), (changing from 8% of the volume of 30%) altering the cavity configuration to a subaortic outflow tract lined by the smooth septal wall (Figs. 4 and 5) (16, 17, 26). Estimates have been made (21) that 15% of the ventricular volume is produced to the mitral valve, as opposed to 5% in diastole, is taken up by the papillary muscle mass. The larger papillary muscle volume in our studies probably reflects the relatively small size of the heart in calcium rigor. Variations exist in amount of trabeculation (22).

Contrary to the view which characterizes the right ventricle solely as a volume pump, evidence can be cited that it is in fact a pressure generator (14). Architecturally the sinus is like the left ventricle; the conus with its small radius of curvature (6:1 ratio) has a mechanical advantage over the sinus fibers (3, 4), both regions having similar wall thicknesses, and it may be considered a pressure regulator (19, 32). At the region of transition between sinus and conus (Fig. 7, no. 2) a sharp delineation of inflow and outflow tracts is created across the right ventricular wall; this represents a functional separation of inflow tract from outflow tract.

Functional studies proved that fiber orientation is a primary factor in determining the capacity of the ventricle to generate pressure. Since the integrity of muscular activity remains unaltered when an incision was placed in the direction of the circumferential fibers but is grossly altered if the fibers are cut across their axis, the right ventricular conus demonstrated that the myocardium contracts in the line of its fibers as perceived by Harvey (7) in 1628. In nine species of mammals, careful dissection of ventricles has essentially confirmed the older literature and denied modern concepts of separately contracting myocardial layers, thus allowing easier understanding of myocardial mechanics.

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REFERENCES


