SPECIAL ARTICLE

Notes on the Muscular Architecture of the Left Ventricle

By Robert P. Grant, M.D.

Nearly three hundred years ago (1669) in his book Tractus de Corde, Richard Lower offered the first detailed description of the muscular anatomy of the ventricle. His drawings show separate overlapping layers, rather like the layers of an onion, each layer consisting of differently directed muscle fibers. Since his day, many anatomists, perhaps most definitively Mall, have repeated his dissections and have altered his schemata only in details. As a result, today the illustrations of ventricular myocardial architecture in all anatomy textbooks are essentially elaborations of Lower’s original drawings. Yet, for generations, medical students (and more recently cardiac surgeons) have compared with dismay the textbook illustrations of the heart with the organ they hold in their hands, for no such layers are to be seen. It is ironic that Lower, who did so much in his day to liberate medicine from medieval dogma, should himself be the origin of a dogma for later generations.

The reason why the Lower schemata fail to be accurate or useful is related to the fact that the only conceptual tool available to him in his day was plane geometry. As he expressed in his Tractus, “according to Geometry’s laws, the straight line is the guide to the oblique. Similarly, the common standard of the straight muscle is the best approach to the study of the circular fabric of the heart.” But plane geometry is inadequate for a three-dimensional network problem, which is what left ventricular myocardium poses. The ventricular myocardium is a syncytium, and a given fiber segment has branching connections with other fiber segments in several different directions. Lower, and the anatomists after him, followed only one of these directions in order to create the planes they sought. Statistical study of the branching predilections must be added to geometry for an accurate picture of myocardial architecture.

The problem is illustrated in figure 1, where the branching predilection in the left ventricle is shown to depend upon, among other things, the size of population of epicardial fibers one studies. On the left, relatively small populations of fibers have been peeled, exposing a branching arrangement which forms shelving overlappings winding in a tight, clockwise, helical course toward the

From the Office of International Research, National Institutes of Health, Bethesda, Maryland.

*Vesalius had pointed out more than a hundred years earlier that the ventricles consisted of separate fibers which, he believed, united at the apex. The most recent exposition of the classic approach to left ventricular anatomy is that of Puff, which contains also an historical review of the subject.
apex. In the middle dissection, a larger population of fibers has been followed, starting from the same epicardial region. A similar clockwise helical path is produced; but it is a much looser helix, reaching the apex in two or three turns. Finally, in the dissection on the right, a still larger population was followed which reaches the apex in a single turn. (In this dissection, one of the Lower-Mall “bundles” was dissected; a direction of branching was deliberately followed which reaches the apex in one turn, where it invaginates, and courses helically upward along the left side of the septum to insert into the AV ring.) These dissections show that while the epicardial left ventricular fibers follow a predominantly helical course, clockwise from base to apex, even within this arrangement there are different branching prevalences.

Of course, in preparing the specimens, most branchings with directions markedly different from that being followed were sundered. A major alternative branching direction when one peels clockwise, well shown in the middle dissection, runs superiorly. It belongs to a helical continuum with a direction generally opposite to that of the helix just described. From the point of view of base-to-apex pathway, it winds counterclockwise instead of clockwise. The clockwise helix predominates among outer layers, while the counterclockwise helix predominates in internal layers. However, the two are completely continuous with each other, and the transition of predominance from one to another is gradual from epicardium to endocardium. Superiorly directed branchings, belonging to the counterclockwise helix, were also evident in the first dissection, but the helix is too tight for them to be apparent in the photograph. For the third dissection, all branchings irrelevant to creating the Lower-Mall bundle were severed. However, the limb which sweeps down to the apex can be said to represent a path in the outer helical system, while that coursing back from apex to base of the AV ring represents a path in the inner, counterclockwise system. This was certainly the most difficult—and the most artificial—of the three dissections.

In problems involving statistical variables,
one approach is to construct models for different degrees of generalization of the problem. No single model gives the whole story, but together they provide a schema. For example, at one extreme in generalization, one can describe over-all arrangement of all fibers, fully realizing it is only a predominant orientation. Then, at the other extreme, one can describe the average branching orientation of a typical, single myocardial unit. Between these two lie many other models of the syncytium, showing regional or transitional branching prevalences. A broad, over-all schema has already been outlined, and one can say that the left ventricle is characterized by an outer clockwise helical system and an inner, counterclockwise helical system, when viewed base-to-apex. This is diagrammed in figure 2, which also demonstrates that the two helices are continuous longitudinally (better shown in the smaller diagram at the right, where the outer layer of the helix has been topologically everted). The two helices are also continuous with each other laterally. This is not shown in this diagram, for it belongs to other schemata, other generalizations. Also overlooked are the specialized branchings at

Figure 2

Schema of a predominant, over-all pathway of fiber continuity in the left ventricular syncytium. It follows a roughly 360-degree clockwise path in the epicardial layers from the base to the apex, and another clockwise path of roughly 360 degrees in the inner layers of the ventricle, back from the apex to the base. Right, a topological eversion of the outer layers of the left ventricle is drawn to demonstrate the fiber continuity longitudinally between the two helical pathways. Lateral continuity also exists but is not shown in the schema.

Figure 3

Schema of the fiber-to-fiber relationship which appears to obtain typically in the left ventricle. While the "fibers" are parallel, by their branchings they form "planes" which appear to rotate.

particular regions of the left ventricle (for example, the vortex at the left ventricular apex, the right-angle branchings at the bases of the papillary muscles, the interdigitating of right and left ventricular muscle, etc. Excellent photographs of some of these regional variations have been published by Puff). Finally, it does not show asymmetries and variations in the helices themselves. For example, as can be seen in the middle dissection, in general the inner helix is steeper in the septum than in the free wall of the left ventricle. Reduction of the syncytium to two helices is indeed a generalization.

At the other extreme in generalizing—the behavior of an individual unit—one also finds a helical orientation. That is, the left ventricular fibers have a twisting relationship to one another. Lower recognized this, for, while he was strongly tempted to describe the fibers of the heart as extending from base to apex like threads, and hoped that following an individual fiber might be like unrolling a strand from a ball of string, he pointed out that this did not take place and that, instead, the fibers, "having gone a little way, seem to twist under the preceding fibers and are at once lost from view." The fiber-to-fiber twist is found through-
out the left ventricle and appears to be in a clockwise sense, viewed distally. One possible way in which fibers which appear to be parallel can, at the same time, form planes of fibers which appear to twist, is shown in figure 3. The prevalence of fiber-to-fiber helical behavior is also evident from the dissection in figure 4. The interesting feature of this dissection is that, on peeling individual strands, the direction of twist appears to be opposite depending upon whether one peels the strand clockwise or counterclockwise.

In summary, the myocardial syncytium has, as one of its architectural properties, many “generations” of twist, from a fiber-to-fiber twist to an over-all, general helical path of external and internal masses of fibers. In a limited sense, this is analogous to the structure of a large rope or hawser. A hawser consists of several ropes twisted helically around each other; each of these ropes, in turn, consists of smaller ropes twisted helically about each other, etc., down to the individual strands of hemp which are also twisted about each other. But there is an important difference between the “generations” of twist in a hawser and those in a section of myocardium. In the hawser, each “generation” can be separated and isolated from the others; in the myocardium there is a smooth syncytial continuity between the smallest to the grossest “generation.” It is little wonder that some bizarre and complex arrangements of muscle “bundles” have been dissected from the substance of the myocardium by anatomists in the conscientious belief that they were identifying separate anatomic units.

The analogy to a rope has certain interesting physiologic implications. The reason why rope is constructed of twisting components (which means, it should be noted, that the effective length of the individual strands is shortened, increasing the cost of rope), is that this design distributes tension equally among all strands. While equalization of tension is probably not an important natural-selection reason why the left ventricular syncytium is helical, no doubt such an architecture does equalize the distribution of its systolic and diastolic tensions. But one of the costs of the twisted structure of rope is that this greatly increases the frictional heat it develops when taut. Little is known about the frictional consequences of myocardial contraction, but undoubtedly some of the energy of contraction is dissipated through friction. Indeed, it has been suggested that one of the ways in which digitalis improves myocardial contraction is by, in effect, reducing myocardial frictional resistance on contraction. Because of considerations such as these, the most important feature of left ventricular architecture to the physiologist may well be the helical design of its syncytium.

A complex helical array is, then, the model of the left ventricular architecture which emerges from combining the two extremes of statistical generalization. But between these two views, one, of the myocardium as a whole, the other the myocardium as represented by single fiber units, several other intermediary and specialized models are possible. The question arises if, among them, there is preferential branching to be found which might permit one to speak, if only loosely, of separate “muscle bundles” of the type Lower and his followers described. This can only be answered after detailed study is done of the statistical prevalence of different branch-
ings at various parts of the heart. I suspect that there are regional differences in the prevalence of branchings of particular types. However, as far as human and canine myocardium is concerned, I doubt if the regional prevalence will prove to be statistically sufficiently predominant and independent of the rest of the syncytium to warrant treating them as anatomically separate “bundles,” much less as physiologically separate “bundles.” I am especially skeptical that the longer “bundles,” those which are described as sweeping down one wall, invaginating at the apex and coursing up the inner wall, shall ever be shown to be relatively independent, coherent anatomic units. My skepticism is heightened by their implausibility from an embryologic point of view, which we shall now turn to.

How did the helical pattern of the left ventricular syncytium come about and, more particularly, why do the outer layers follow a generally different path from the inner layers? The first question may not be a difficult one when considered in its generality. Myocardium grows by incomplete lateral splitting of fibers, with the “split” several times longer than the diameter of the father fiber. By this mechanism, unless other factors intervene, myocardial growth is characterized by increasing numbers of fiber units which are more or less parallel with each other, joined into a continuum by extremely acute-angle branchings. The branchings are so acute-angled, indeed, that it is impossible to say which is “fiber” and which “branch.” This type of growth would inevitably result in a matrix where fibers appear parallel yet, at the same time, intricately embrace each other.

But the network one discovers on dissection is not random in its branchings. Indeed, as has been shown, it is so systematic that an over-all, generally helical pattern can be discerned. This must mean that certain directions of branchings become thicker with growth than others, establishing systematic pathways of principal fiber continuity. One way this might come about is related to the fact, well known from studies of experimental hypertrophy, that the thickness of a fiber is a function of the amount of tension it experiences. From this principle one might suggest that, during growth, those fibers (and branchings) which are more parallel with the mechanical vector generated in the left ventricular wall during systole, become thicker than others. They reach a critical diameter and then split in parallel, thus establishing the preferential paths of fiber continuity which are observed. It appears to be the obliquely directed fibers and branchings which undergo this preferential thickening, giving left ventricular fiber continuity a relatively systematic helical course.*

The explanation for the difference between the direction of the outer and inner helices may be embryologic, related to the change in the function of the left ventricle between the time when fibers develop in the epicardial layers and when they appear in more endocardial regions. In earliest fetal stages of development, the ventricular wall consists of densely trabeculated, sponge-like myoblastic tissue. The first region where the myoblasts differentiate into striated fibers is in the outermost, epicardial layers of the left ventricle. These first fibers have an obliquely horizontal lie similar to that in the adult heart shown in the upper dissection of figure 1. At this stage of heart development, the four chambers are in tandem, with the left ventricle empty-

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*It is always wise to start with a simple theory, fully expecting it to prove inadequate with further knowledge. This is certainly true of efforts to explain myocardial architecture. For example, while it is generally true that myocardial growth produces generations of relatively parallel fibers, we have a striking exception to this in the outflow tract of the right ventricle. In this low-pressure region of simple cylindrical design, there is an amazingly complex collection of differently directed muscle “bundles.” Right-angle branchings are common, and fiber groups in markedly different directions directly overlie each other with few transitional forms. To be sure, it is well known that the outflow tract of the right ventricle is embryologically, phylogenetically, and functionally quite different from the remainder of the ventricular myocardium, and it no doubt follows different growth imperatives. Nevertheless, its unexplained complexity should urge caution for any simple theory of the development of cardiac architecture.
ing laterally into the right ventricle through the interventricular canal. Thus, the first fibers to develop have a lie which is relatively parallel with the path of ejection of the left ventricle. This is also the most efficient lie from the mechanical point of view. Many years ago, Weiss' showed that when rhythmic mechanical tension is applied to a colony of undifferentiated fibroblasts, the collagen fibers are laid down parallel with the direction of the tension. And Weibel² has found that the smooth muscle of a vein can be caused to proliferate parallel with the direction of an imposed rhythmic mechanical tension. Similar experiments have not yet been done with myoblastic tissue. Nevertheless it is interesting that the lie of the earliest myocardial fibers is consistent with this principle.

By the time the inner regions of the left ventricle first begin to develop a fiber architecture, the left ventricle has changed considerably. It is much larger; the interventricular canal is a relatively small aperture in the upper region of the septum; and the aorta is becoming the principal pathway of ejection. With the change in direction of ejection, it is not surprising that the endocardial myoblastic tissue gives rise to fibers with a quite different direction from that of the epicardial fibers. Furthermore, since the change in function is a gradual one, one might expect the architecture to be rich with transitional and modified fiber patterns.

An especially interesting part of the left ventricle is its apex. Here the ventricular fibers form a vortex of elegantly simple and symmetric design, as shown in figure 5.¹ The simple, symmetric design recalls one of d'Arcy Thompson's⁸ injunctions: morphology of an organ should be seen as a graph; just as, for a graph, the fewer and the more constant and equal the variables the more symmetric the graph, so in growth, the fewer and more constant the external factors influencing cell multiplication, the more symmetric the organ. The symmetry of the apex of the left ventricle illustrates this, for the most important external variable influencing myocardial growth is the mechanical tension of contraction. However, because of the hemiovoid shape of the left ventricle, the mechanical tension of contraction is least at the apex, as has been frequently pointed out by others. This not only explains the simplicity of the apical architecture but also why the apex is so thin, being but a fraction of the thickness of the lateral walls of the ventricle.

Furthermore, the apex is probably the oldest part of the left ventricular muscle embryologically. This follows from the fact that, in general, in a syncytial tissue which grows by fission of its elements, its increase in mass will be logarithmically greater at the periphery (just as branchings of tree are logarithmically more numerous peripherally). For the left ventricular myocardium, its "periphery" is the base of the ventricle, and this is where the

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¹By definition, a vortex should have a single umbilicus. As can be seen in the figure, the apex of the left ventricle has two umbilici, about 4 mm. apart, which become a single vortex barely two or three fiber layers beneath the epicardium. The right ventricle has its own vortex, consisting of a single umbilicus.

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Figure 5

Left. Apex of the left ventricle of the dog heart, showing the bi-umbilicate vortex. Right. Branching connections which come off the helix to course internally where they form a subendocardial, thick vertical column which inserts into the lateral fibrous trigone of the left ventricular AV ring. The helix has been peeled down toward endocardial regions. The right-angle branchings from the helix are shown to occur all along the length of the left ventricle. A similar array of right-angle branchings can be demonstrated on the other side of the left ventricle, forming a similar vertical column leading to the other fibrous trigone in the AV ring.
increase of mass of the ventricle during growth principally takes place. The apex, on the other hand, is the region where least fission has taken place.

The umbilation at the apex is the expression of the difference in direction of the two helical systems, the inner and outer. This is demonstrated by the earlier topological diagram, in figure 2. In d'Arcy Thompson's terms, the umbilation is, as it were, the “point of inflection” between the two helical graphs.

In schematizing the left ventricular architecture, the tendency, here as elsewhere, is always to oversimplify it. The syncytium is replete with regional and local variations and deformations which depart from over-all, generalized patterns. For example, right-angle and tri-cornuate branchings are encountered at the base of the heart and especially in the region of the membranous septum where fiber coupling is especially complex. They are also seen where the free wall of right ventricle interdigitates with the left ventricle. Another regional variation in the left ventricle which may be of considerable physiological importance, yet is infrequently noted in textbooks, is illustrated in figure 6. The left ventricular syncytium has two prominent columns parallel with the long axis of the ventricle, each inserting into one of the two fibrous trigones of the left ventricular AV ring. The vast majority of endocardial fibers finally, directly or indirectly, inserts into one or the other of these trigones. But the substance of the two vertical columns which the trigones subtend is actually formed by prominent right-angle branchings from both helical systems, all along the length of the left ventricle, as shown in the figure. The two columns are quite separate from the two papillary muscles; their physiological importance and embryologic origin are quite unknown.

Conclusions

The search for an accurate and detailed picture of the muscular architecture of the left ventricle is by no means a trivial goal. Cardiac physiologists now describe cardiac energetics in terms of fiber length and unit-fiber shortening; for this they must have an accurate model of fiber orientation. A decade or so ago, some thundering errors were committed in the study of the spread of excitation through the heart as a result of too literal acceptance of the Lower-Mall schema. And today, there are a number of problems in cardiology which demand an adequate model of ventricular architecture for their solution; for example, the morphologic explanation of subaortic muscular hypertrophy; the consequences upon myocardial contraction of the muscular defects in congenital heart diseases such as ventricular septal defect; the morphogenesis of ventricular hypertrophy, etc.

Statistical methods must be added to those of geometry for developing a picture of left ventricular architecture. Any single schema offers only one dimension of the problem, one degree of generalizing. This, perhaps, is the main defect of the Lower-Mall schema, for it overlooks the fact that the human myocardium is, before anything else, a syncytium. The present study has endeavored to approach the problem from the two extremes of generalization—the fiber arrangement as seen in the heart as a whole, and the fiber arrangement of one fiber to another. Statistically established models between these two extremes of generalization are needed for a complete picture of left ventricular architecture. Conjectures are offered to explain the over-all helical design of the left ventricular syncytium, the simple geometry of its apical vortex, the difference in general fiber orientation of internal versus external fibers, etc. Perhaps the most striking feature of these conjectures is how easily they (and others) can be tested by quite simple technics of experimental cardiac embryology, a field which is quite undeveloped and holds great promise for answering important questions in clinical cardiology.

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ROBERT P. GRANT

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