THE SPREAD OF THE EXCITATION WAVE
IN THE OVINE LEFT VENTRICLE

DISSERTATION

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The nature of the spread of the excitation wave through the ventricular musculature of the heart has long been a subject of experimental study. Current concepts of the nature and manner of propagation of the excitation wave in mammalian ventricles stems from the pioneer work of Lewis and Rothschild. The observations of these two workers was later corroborated by Wilson and co-workers. Recently, the concepts of the spread of the excitation wave has been modified by Rothman, Kennamer et al.

The original hypothesis formulated, which has been accepted for more than twenty years, was as follows: the depolarization impulse travels rapidly along the endocardium from septum to apex, then from the apex to the base, via the Purkinje fibers. It proceeds through the ventricular wall from the endocardium to the epicardium via muscle pathways at a steady, constant rate. Lewis and Rothschild calculated the rates of depolarization in Purkinje fibers as 4000 to 6000 millimeters per second, and in ventricular muscle as 400 to 600 millimeters per second.

More recent concepts by Prinzmetal, et al. modify the original hypothesis as follows: the depolarization
impulse travels very quickly through the Purkinje network into the depths of the myocardium approximately one-half to two-thirds of the ventricular wall toward the epicardial surface. It proceeds through the remaining ventricular wall by muscle fiber conduction at a slower rate. This outer layer conduction is responsible for the major portion of the deflections seen in the electrocardiographic leads.

If either of the concepts are accepted, the mean spatial vector forces generated by the heart can be correlated to the common limb and chest leads used by electrocardiographers. In both man and dog there is good correlation between the leads taken and the anatomical position of the heart. However, if standard limb and chest leads are taken in cattle, sheep, and some other ungulates, and subjected to vector analysis, correlation cannot be made. Measurements of the mean spatial vector force of the QRS complex is approximately 180 degrees opposite man and dogs.

Explanations for this phenomenon have been proposed, but little experimentation has been undertaken to solve the problem. Kisch recorded epicardial and ventricular cavity electrograms from four calves. He suggested that the excitation wave may spread from the epicardium toward the endocardium. Alfredson and Sykes produced bundle branch block in eighteen calves. Their
results suggested that the conduction system of the calves' heart contributes to the rapid excitation process. Direct exploration of the sheep's heart has not been reported.

To more effectively interpret electrocardiograms of ungulates, specific information on the genesis of the deflections recorded must be known. Because of the similarity of conventional electrocardiograms of sheep and cattle, information gained in experimentation with sheep may be applicable to cattle, and perhaps other ungulates.

The present investigation was undertaken in an attempt to obtain information concerning the genesis of the electrocardiographic recordings seen in sheep. The objectives were as follows:

1. To determine the mean spatial vector forces generated by activity of the ovine myocardium.
2. To determine the instantaneous vectors which are responsible for the deflection recorded in standard leads.
3. To study the epicardial surface of the left ventricle relative to time of onset of depolarization.
4. To study the epicardial and endocardial surfaces relative to the configuration of deflections.
5. To determine the time of activation of the endocardium, myocardium, and epicardium, by synchronous
recordings.

6. To determine the spread of the activation wave in the musculature of the ovine left ventricle.

7. To establish, if possible, an anatomical basis for the depolarization process.

The left ventricle was chosen because it is the largest muscle mass of the heart and therefore contributes the major bio-electrical force. Also, it was chosen to limit the problem to a specific area which could be studied completely.

The accuracy of diagnosis of disease conditions depends upon the observer's knowledge of the normal. This involves not only the superficial but also the detailed genesis of the phenomenon observed. It was hoped in this study to determine the cause of each of the instantaneous deflections recorded by standard techniques in electrocardiography. Once this was known, abnormalities could be recognized, and the cause and effect relationship become more comprehensible.
REVIEW OF LITERATURE

In 1922 Nörr published the first report on the characteristics of the electrocardiogram of the sheep and goat. He used lead III in the sheep. The results of this lead were primarily negative deflections.

In 1938 and 1939 Nörr studied the electrocardiogram of a flock of sheep in which a 62 per cent mortality had occurred. Using an axial lead similar to that devised by Strohmaier, negative deflections were recorded. The principal electrocardiographic abnormality was the occurrence of premature ventricular systoles. Calcium deposits were found in the myocardium at necropsy.

In 1939 Strohmaier attempted to determine the most suitable electrode placement and type of electrode to use on sheep and goats. The results of his study indicated that an axial type lead, using needle electrodes was most suitable. In this type of lead the major ventricular deflection was always negative. In most of the animals the major negative deflection was preceded by a small positive deflection. His results indicate that the major ventricular vector is directed away from the sternum anteriorly and dorsally.

In 1944 Louisada et al. studied the electrocardiogram of two sheep and one goat, using an axial lead
similar to that described by Strohmaier. His records show the ventricular complex to be composed of a small r followed by a large S wave. This would indicate that the major vector force of ventricular activity was receding from the exploring or positive electrode attached to the left sternal region.

In 1948 Mullick et al. studied the influence of thyroidectomy and thyroprotein replacement therapy in sheep. The standard limb leads were used in the experiment. The form of the ventricular complexes were of low amplitude. The authors found it difficult to measure changes because of the unsatisfactory nature of the records.

In 1953 Bacigalupo et al. studied twenty-three male lambs. The three standard limb leads were used. Leads II and III are shown in his report. Both records were of the QS type, indicating that the spread of the excitation wave was receding from the positive exploring electrodes attached to the left hind limb of the animals.

In 1948 Platner et al. recorded electrocardiograms from twelve one- to six-year-old sheep. Leads I, II, and III were used. His records show primarily negative deflections in lead I of the QS type. Lead II was frequently negative or diphasic. Lead III was diphasic. All were of low amplitude. The records indicate that the mean spatial vector of the major deflection was directed
upward and away from the posterior extremity of the animals.

In 1955 Dukes discussed Souza's work on the effects of calcium on the electrocardiograms of sheep under pentobarbital sodium anesthesia. The records show QS deflections in lead II of the normal sheep prior to the administration of the anesthetic agent and the calcium.

There were no reports in the literature of vectorcardiograms or direct electrogram studies of the sheep.

Electrocardiographic Studies of Some Other Ungulates

In 1928 Lautenschlager studied methods of recording the bovine electrocardiogram. At Nörr's suggestion he used an axial lead in which the positive electrode was attached on the left side of the chest in the fifth intercostal space at the level of and directly behind the olecranon. The negative electrode was attached on the right side of the body, a handsbreadth in front of the cervical angle of the scapula. When using this lead, negative QS deflections were recorded. The duration of the ventricular complex was 0.08 to 0.10 of a second.

In 1937 Biber studied the electrocardiogram of twenty-four cattle. He stated that the standard limb leads do not always yield satisfactory electrocardiograms.

In 1940 Sykes and Alfredson studied the electro-
cardiographic changes on four calves subjected to a low potassium diet. Four more calves were used as control animals. Standard limb leads were used in the study. The control records were QS deflections in leads I and II. Lead III was bizarre. The duration of the QRS complex was from 0.06 to 0.12 of a second. During the period of study on the potassium deficient calves, the duration of the QRS complex increased up to as long as 0.24 of a second. The configuration also changes. In leads I and II qR deflections were recorded. RS deflections were recorded in lead III. On autopsy, pathological changes were not restricted to any one region of the heart.

In 1940 Sporri and Raggenbass studied the electrocardiograms of cattle using the axial lead similar to that described by Nörr and Lautenschlager. The major QRS was always negative. The duration of the QRS varied from 0.065 to 0.12 of a second, with a mean of 0.095. The authors commented on the difficulty in measuring the QRS complex.

In 1942 Alfredson and Sykes recorded electrocardiograms on ninety-seven normal dairy cattle at monthly intervals for three months. This study represented the most extensive of any made in the United States. The authors noted that the bovine electrocardiogram resembled the human in only one respect. The interval lengths
(0.06 to 0.12, mean 0.09) were nearly alike in the two species. This indicated to them that, considering the greater mass of the bovine heart, the spread of the impulse was relatively faster in this species. They also noted that the potentials were smaller than in the human heart. They attempted to establish a normal QRS electrical axis, using the system applied to the standard limb leads of man, but were unable to do so because of the variability of the types of deflection within the species and individuals. Examination of their records reveals both negative and positive complexes in all three standard limb leads.

In 1944 Louisada et al. studied the electrocardiograms of two cows and two bulls. They used both the standard limb leads and an axial lead similar to that described by Nörr and Lautenschläger. The records shown in their paper were of the axial type. All were strictly negative deflections. The duration of the QRS was 0.05 to 0.08 of a second.

In 1948 Platner et al. obtained electrocardiograms from ten dairy cows and thirteen dairy calves, using the standard limb leads. His records show variable type QRS complexes, ranging from negative to positive in all leads.

In 1948 Kisch et al. studied the electrical activity of five calves' hearts. They examined the
hearts by standard limb leads and direct electrograms from the endocardial and epicardial surfaces. The standard limb leads showed extremely low voltage deflections in lead I, some of which were almost isoelectric. Leads II and III were remarkably similar in appearance. Both were negative deflections. A QS was present in three of the animals on both leads. In the other animals an rS was recorded. The duration of the QRS complex was approximately 0.06 of a second in the standard limb leads.

Direct electrograms were obtained by opening the chest under anesthesia and artificial respiration. The endocardial leads were made with an electrode-tipped catheter visualized by fluoroscopy as to location in the cavity. The accuracy of this method is not always what is desired. Epicardial leads were taken from the pericardial surface and directly from the epicardium. Simultaneous epicardial and endocardial leads were taken for timing purposes.

The epicardial electrograms revealed rS and QS deflections from the surface of both the right and left ventricles, excepting at the base, where they converted to Rs and qRs deflections. Electrograms from above the base were all positive in character. The endocardial electrograms were remarkably different from other animals studied. The deflections were primarily positive. In
the right as well as the left ventricular cavity, qR, Rs, and qRs deflections were recorded. In one animal in which the electrode catheter was observed to be in the apical region, they record negative deflections.

Synchronous time relationship studies using lead II as a reference revealed a sequence of intrinsic deflection patterns. The sequence was: right ventricular apex—left ventricular apex at the same time as at the right ventricular center and left ventricular center—right ventricular base (near right margin)—left ventricular base—center of right ventricular base and area near pulmonary artery and wall of the pulmonary artery—wall of the aorta.

Endocardial-epicardial synchronous recordings showed that the onset of the intrinsic deflection occurred almost synchronously in the free wall of the left ventricle. The left apical epicardial intrinsic deflection occurred before the left cavity potential. These authors commented on the distinct difference of endocardial and epicardial electrograms of the calf compared to some other mammals and man. They suggested that this difference should be reflected in chest leads. This proved to be the case when they ran chest leads on another calf. They ran CR chest leads up to the fifth intercostal space. All leads were rS or QS deflections.

The conclusion was that the results obtained from limb and chest leads could not be a consequence of a
specific position of the calf's heart in the chest, but may have been due to a conduction pattern different than that which occurs in most of the other mammals, including man. They questioned whether the results reported were typical of full grown cattle, or are present only during the first days of life of the calf.

In 1953 Smith studied the effects of hypervitaminosis D and traumatic pericarditis on the bovine electrocardiogram. Twelve cows and two calves were used in the experiment. Standard limb leads I, II, and III were recorded on all animals. Unipolar leads AVR, AVL, and AVF were also recorded on the animals in the latter part of the experiment. In addition to the limb leads, ten unipolar chest leads and one bipolar chest lead (axial lead) were registered on cows in the latter phases of the study. On the illustration of typical leads in cattle shown in his work, lead I shows a negative QRS complex. Lead II is a negative deflection and lead III bizarre. In the unipolar limb leads AVR is positive, AVL negative, and AVF a diphasic QR type deflection. The chest leads on the left side were negative QRS complexes up to a point about five inches above the point of the olecranon in the fifth intercostal space. Above that point the deflections converted to diphasic, then positive deflections. A Q wave was present on all recordings on the left side. On the right side a diphasic
RS deflection was recorded at the point of the olecranon. Above this point, positive deflections were found. The axial lead was the most consistent of all the records made. It consisted of a very small r wave followed by a deep S wave.

In 1940 Alfredson and Sykes investigated the electrocardiographic changes resulting from section of either the right or left bundle branch in young calves and dogs. This study was undertaken because the authors suspected that there may have been major differences between the intraventricular conducting system of the ox heart and that of the canine heart.

They also stated that in comparison with the canine and the human heart, the ox heart is very much heavier and its wall much thicker. Therefore, it would be expected that the QRS interval of the ox would be much longer than that of the dog or of man. In a previous study by the authors, it was found that such was not true. The mean duration of the QRS was 0.09 of a second.

They sectioned the bundle branches of fourteen calves and ten dogs. Measurements were made of the QRS interval using lead II throughout, since they considered this lead the most satisfactory. The average increase in duration when the right bundle branch was sectioned was 0.013 of a second, with little change in the configuration. When the left bundle branch was severed
an average of 0.005 of a second increase in the duration QRS was found. In the records shown, there was a marked change in configuration of the three standard limb leads following section of the left bundle branch. Lead I, which was previously a qR deflection of low voltage, changed to a large R of higher voltage. Lead II was an rs deflection. It changed to Rs deflection of greater magnitude. Lead III was an rS deflection which changed to an RS. Although the authors did not use vector analysis in interpreting the changes, the records show a shift of approximately 180 degrees in the vector direction.

The results of their experiment suggested that there is a decided difference in the distribution of the intraventricular conduction system between the dog and the calf. They stated that it was difficult to understand how the cardiac impulse could spread so quickly over the ventricular musculature of so large a heart, if it spreads with approximately the same speed and in the same manner as in the human and the canine heart. It was their contention that the Purkinje system was responsible for this rapid conduction.

The work of Kisch et al. and Sykes and Alfredson represents the only experimental work on ungulates directed toward determining the manner of excitation in the myocardium. There have been no reports of vectorcardiograms in cattle.
Of all the ungulates studied electrocardiographically the horse has been the animal most reported in the literature. It is beyond the scope of this paper to review the literature on that animal. Suffice to say, the horse electrocardiogram is not like that of man or dog, nor is it very similar to sheep and cattle, but falls into a classification between the groups. Positive deflections are frequently recorded in the limb leads. However, in the axial lead it is a very similar one to that found in cattle and sheep, being primarily a negative deflection of the rs type.

The pig is one ungulate which is similar to the dog in the electrocardiographic recordings made from the limb leads. Very little has been reported on the pig. Smith made electrocardiographic recordings on over one hundred pigs. Lead I was primarily a positive deflection. Leads II and III were almost universally high positive deflections.

Electrocardiographic Studies of the Dog

More experiments and electrocardiographic studies have been reported on the dog than on any other domestic animal. In this review the writer will present only articles which have direct application to the process of depolarization in the ventricular musculature.

In 1915 Lewis and Rothschild reported the results
of their study of the excitatory process in the dog's heart. Much of the terminology, and many of the techniques used by the present day workers stems from this report. The terms intrinsic and extrinsic deflection were originated by these workers. The unipolar technique was described and used by these authors. They were the first to suspect that there was some relationship between the Purkinje system and excitation process in the ventricular musculature.

In their study the form of the epicardial leads from the surface of the left ventricle consisted of a small q followed by a large R wave. The peak of the R was used as the onset of the intrinsic deflection and the point at which they made time measurements. The entire surface of the ventricles was mapped out relative to the time of onset of the arrival of the excitation. They concluded from this phase of the study that the excitatory process did not follow the anatomical direction of the muscle fibers. The spread along the surface appeared to follow a large number of distinct channels, the nature of which was suggested by the location of the Purkinje system. To establish proof that the system was a functional unit they performed two groups of experimental procedures. First, they cut the bundle branches and produced a distinct change in the time of onset, duration and configuration of the leads. Second,
they made cuts in the form of a square into the ventri­
cular musculature approximately ten millimeters deep and made recordings in the center of the square. The re­cordings were the same in duration and configuration as control recordings.

These authors concluded that the spread of the excitation process was dependent upon the Purkinje system. The excitation impulse traveled rapidly (4000 to 6000 millimeters per second) along the endocardium from septum to apex, then from apex to base by way of the Purkinje system. The impulse then spread through the ventricular wall from the subendocardium toward the epicardium by muscle fiber to muscle fiber pathways at a slower (400 to 600 millimeters per second) but steady, constant rate.

In 1931 Wilson et al. corroborated the findings of Lewis and Rothschild. They concluded that the direction of the electrical axis of the heart was determined by the direction in which the excitation process was advancing.

In 1934 Wilson et al. investigated the unipolar electrogram of the ventricular surface and ventricular cavity. In this study they attempted to prove the validity of the unipolar technique in addition to the configuration of the recordings made in and on the dog's heart. Epicardial leads were reported as a small initial
negative deflection followed by a large and rapid positive wave. The small initial negative deflection was attributed to activation of the endocardium and the main positive deflection due to the progressive excitatory process outward. The left ventricular cavity potential was negative throughout the excitation cycle.

In 1947 Wilson et al. published an extensive review of the ventricular complex of the electrocardiogram. In their paper they concluded that: (1) the interventricular septum was activated from left to right; (2) normally the excitatory process reached the ventricular musculature by way of the Purkinje system; (3) excitation of the subendocardial muscle began in many different points simultaneously, and many islands of active tissue originated and coalesced to form larger islands; and (4) the endocardium was primarily electrocardiographically negative. The epicardium was electrocardiographically positive.

In 1950 Sodi-Pallares et al. studied the relationship between the intrinsic deflection and subepicardial activation in the dog's heart. They concluded that in unipolar leads the lowest part of the intrinsic, or its lower third, corresponded to the arrival of the wave of activation in subendocardial muscle. In bipolar leads, the greatest and most rapid deflection corresponded to the activation of the small muscular region in contact
with the electrodes.

In 1951 Kisch studied the influence of extrinsic activity on direct leads from the surface of the dog's heart. He concluded that leads taken from exposed hearts gave a high degree of reliability.

In 1952 Burchell et al. studied the spread of the excitation through the ventricular septum of the dog's heart by removing the ventricular walls and applying copper electrodes to the septum. In addition to the scalar electrograms, vectorgrams of the septum were made. They came to the conclusion that in the hearts they studied the activation of the interventricular septum was from apex to base. This is in contrast to the generally accepted theory. In addition to the statement concerning septal activation, they stated that the excitatory process in the dog's ventricle is a very complicated process and does not follow the stereotyped and conventional bundle branch and Purkinje system.

In 1953 Durrer et al. studied the spread of activation in the left ventricular wall of the dog. Several different techniques were used by the authors. Bipolar differential, transmural, and unipolar electrograms were made at various levels of the myocardium. Spatial orientation studies of the results were reported. These authors concluded that: (1) activation of the inner layers was simultaneous, and this was most likely effected through the Purkinje system within that area; (2) the
shape of the activation front was not regular, as the activation spread rapidly in the inner layers but not in the outer layers; and (3) the angle of the front in the outer layers was small and depended upon the thickness of the wall.

In 1953 Kennamer et al. studied twenty-three dog's hearts using epicardial, endocardial and plunge electrodes. Of the left ventricles studied, positive potentials were found to predominate only in a superficial layer constituting approximately twenty per cent of the intramural myocardium. The innermost eighty per cent of the wall was primarily or entirely negative depolarization waves.

The distribution of intramural potentials was also studied by inactivating the outermost one-fourth to one-third of the left ventricular wall by cautery and excision of that region. Direct leads from the inactivated surface were consistently less positive than control records of the same area.

They also measured the velocity of depolarization. It was found to be considerably more rapid in the innermost two-thirds of the wall than in the superficial layers.

As a result of their findings they concluded that the disproportionate negativity and inconstant velocity may be related to the presence of the Purkinje system.
In 1953 Scher et al. using a sixteen channel oscilloscope to record synchronous activity of the myocardium, studied thirty dog's hearts. The results of their study revealed that through most of the ventricle, rapid subendocardial activation is followed by slow spread perpendicular to the epicardial and endocardial surfaces. They suggested that the rapid subendocardial spread may be via the Purkinje tissue.

In 1953 Prinzmetal et al. studied intramural depolarization potentials in myocardial infarction. In the control records shown in his report, approximately eighty per cent of the ventricular musculature exhibited predominantly negative depolarization potential. Positive potentials prevailed only in the epicardial layer of the ventricular wall. Destruction of the epicardial surface responsible for the R waves resulted in surface QS waves.

In 1954 Rothman et al. studied the genesis of the depolarization complex in the dog's heart. All of the forty-four dogs studied yielded positive deflections from the epicardial surface. The time of arrival of the depolarization process at various levels of the ventricular wall were studied. The depolarization process was found to pass almost instantaneously through the inner layers, rapidly through the midventricular layers.
and relatively slowly through the outer layers. The average rate of depolarization from the midventricular levels to the epicardium was 500 millimeters per second in the free wall of the left ventricle. An explanation for the rapid spread in the inner layers was based upon the distribution of the Purkinje fibers.

In 1954 Kennamer and Prinzmetal studied the depolarization process in normal dog's hearts and in those with bundle branch block. The depolarization complexes recorded from the ventricles during normal intraventricular conduction were as follows. The epicardial surface and subjacent myocardium yielded positive Rs type deflection. In intramural leads from greater depths of the ventricular wall, the R wave became smaller and the S wave grew larger. When the subendocardial zone was reached, purely negative deflections were recorded.

Based on their findings they concluded that in the normal canine heart, the depolarization wave passed rapidly through the Purkinje system before entering the mural myocardium.

In 1953 Durrer et al. studied the spread of activation in the left ventricular wall of the dog's heart. Their findings were similar to the findings of Kennamer and others: synchronous negative complexes in the inner layers and asynchronous complexes in the outer layers. A hypothesis was made that the distribution of the
Purkinje fibers was responsible for the rapid conduction in the inner layers. The outer layers depended upon muscle conduction.

In 1954 Rakita et al. studied the hearts of twenty-one dogs with artificially produced coronary artery occlusion. Normal records were made prior to the occlusion. In the normal records Rs deflections were recorded on the epicardium, rs in the mid-myocardium, QS in both subendocardium and in the cavity.

In 1954 Prinzmetal et al. studied the configuration and speed of conduction in sixty-eight normal and subendocardial infarcted dog's hearts. QS deflections were recorded in the cavity and subendocardium, rS in the mid-myocardium, and Rs in the subepicardium and epicardium. The rates of intramural depolarization were measured by means of cathode-ray oscillograms. Depolarization of the inner ventricular layers occurred at rates of several thousand millimeters per second. In the outer ventricular layers depolarization rates were 300 to 500 millimeters per second.

In 1954 Smith et al. reported electrocardiographic studies performed on twenty dogs before and after bundle branch block was artificially effected. As a result of their study they concluded that certain segments of the ventricular myocardium are supplied by specific portions of the conduction system, without cross connections.
In 1955 Sodi-Pallares et al. reported a study of the conduction rate of the depolarization process in the dog's heart. They found that in at least one-half of the muscle mass proximal to the endocardium, the conduction rate was approximately 2000 millimeters per second. In some of the recordings intramural points were activated before endocardial areas located at the same level, giving the impression that the stimulus approached the endocardium instead of moving away from it.

In 1955 Durrer reported the results of a study on the spread of activation in the left ventricular wall of the dog by spatial analysis. He concluded that the dog's left ventricle consisted of two different layers, an inner layer activated by the Purkinje system and an outer layer devoid of conduction system. Normally the inner layer is activated synchronously. In the outer layers a well-developed front, making a small angle with the epicardial surface is propagated at a velocity of approximately 500 millimeters per second.

**Literature on the Purkinje System**

Lewis and Rothaschild in 1913, in their report on the excitatory process in the dog's heart, discussed the Purkinje system of the bovine heart compared to
that of the dog's. They were the first to describe the Purkinje fibers crossing the ventricular cavity by way of the moderator bands in ungulates. Injection of the conducting system with contrasting media was attempted on both ox and dog hearts. They were able to outline the bovine Purkinje system in some detail but failed to do so in the canine heart.

In 1931 Cardwell and Abramson reported a study of the atrioventricular conduction system of the beef heart. In this report they described a technique of injecting the Purkinje system with diluted India ink. Histological studies were also made of the conducting tissue.

The conduction system of the left ventricle consisted of the main left bundle branch and its arborizations. Two large trunks which cross the ventricular cavity to the base of each papillary muscle are clearly demonstrated. The remainder of the left bundle branch and the two branches to each papillary muscle divide into many branches forming a network over the subendocardial surface of the ventricle except at the base. The subendocardial network was found to branch and form pathways into the myocardium as far out as the subepicardial surface. Branches of the myocardial Purkinje fibers from the left bundle branch in the
interventricular septum were found to make connection with branches from the right bundle branch.

Histological sections of the myocardium revealed a well-developed sheath surrounding the conducting tissue.

In 1936 Abramson and Margolin reported an extensive study of the Purkinje conduction network in the myocardium of mammalian ventricles. The conduction system of the sheep and ox was studied by the injection method and histological section. The conduction system of the dog and pig could not be investigated by means of the injection method because of the impossibility of injection. Histological methods were employed for these two species.

The ventricular myocardial conduction system of the ox and sheep heart was found to be highly differentiated both grossly and histologically. It was characterized by its great width of the cells (five times that of an ordinary muscle fiber) and diffuse distribution of the fibrils which form a syncytium. The conduction system of the dog was found to be poorly developed compared to that of the ox and sheep. Histological differentiation was less marked. The minute anatomy approached that of ordinary myocardium.

The myocardial Purkinje fibers of the sheep were
found to penetrate the muscle substance as far as the epicardial surface, forming plexuses which extended obliquely or roughly parallel to the subendocardial network.
EXPERIMENTAL PROCEDURE

Equipment and Material

The sheep was chosen as the experimental animal for several reasons. First, the electrocardiogram is similar to that of cattle, and some other ungulates. Second, the cost of the animal was not excessive, so that a significant number of animals could be used. Third, because of its size the animal was easy to handle.

The animals were purchased from a sale barn at random, without attempting to choose any specific sex or breed. They were all reasonably healthy and did not appear to be suffering from any disease condition which would affect the results of the study. The age of the animals ranged from approximately two years to twelve years, with the exception of one animal, which was a very aged ewe. There was a total of sixteen ewes, two wethers and one ram used in the experiment.

In addition to the sheep, four dogs were used in the study. The purpose of the dog experiments was to assure that the results obtained with the equipment used was comparable to that reported in the literature. Furthermore, the results on the dogs were used as a comparison with that of the sheep to determine simil-
arities and differences, utilizing exactly the same technique for both animals.

Anesthesia and Artificial Respiration

The anesthetic agent utilized was pentobarbital sodium, administered intravenously until the desired plane of anesthesia was obtained.

Artificial respiration was attained through the use of three types of respirators. The first type used during the early part of the experiment was the modified windshield wiper type. The second type used was the "Seeler" respirator, and the third a "Respirator-Aid" respirator.

All experimental animals were placed on the operating table in a right lateral recumbent position. This position was chosen because much of the previous experimental work has been performed in that manner. Furthermore, in that position the left ventricle could be exposed for exploration purposes.

Electrocardiographic Equipment

The records obtained were recorded with a four-

** Manufactured by Professional Services, Inc., Miami, Florida
channel Sanborn Polyviso and a Sanborn twinbeam electrocardiograph.

The Sanborn Polyviso operated at the maximum paper speed of 50 millimeters per second, twice the standard rate. Deflections obtained are spread out so that each component can be studied in some detail as to timing, magnitude, and configuration. Tracings were recorded at an attenuation of 20X, 10X, and 4X, depending upon the conditions encountered. The original standardization was so adjusted that one millivolt caused a one centimeter deflection. Standardization was checked at the beginning and end of each series of observations. When the Sanborn Polyviso was run at its maximum paper speed, the apparatus was accurate to within 0.02 of a second. The recording paper used in the four-channel Polyviso is of the thermosensitive type which records directly by a heated stylus attached to recording galvanometers.

The Sanborn Twinbeam was operated at the maximum paper speed of 75 millimeters per second, three times the standard rate. Deflections obtained are spread out so that each component can be studied with good detail, especially as to timing. The magnitude and configuration is exceptionally well defined with the photographic recording of this machine. When the Sanborn Twinbeam was run at maximum paper speed it was accurate to within
0.004 of a second.

Vectorcardiographic Equipment

In order to determine the cardiac vectors at any instant with respect to time and space, a vectorcardiographic apparatus is especially useful. Since it was believed that vectorcardiograms would be useful in determining the instantaneous and mean vector forces in this study, an apparatus was designed utilizing the Sanborn Polyviso amplification system. The output of the amplification system was fed into a Dumont cathode ray oscillograph in such a manner that satisfactory Wilson Equilateral Tetrahedral system vectorcardiograms were obtained. The tetrahedral system lends itself especially well to animal vectorcardiography because of their body conformation. The oscillograph screen was photographed with a 35 millimeter Argus camera equipped with a f 2.9 lens. In the later part of the study a time interruption apparatus was used to determine time intervals.

The vectorcardiographic equipment was standardized so that one millivolt produced a 45-degree deflection of three inches on the oscillograph screen. Standardization for dogs was a 45-degree deflection of one inch on the oscillograph screen. It was necessary to increase the deflection to three inches for sheep because of the low
voltage commonly obtained from the electrodes attached to the animal.

Special Design Equipment

In order to record potentials on the epicardial surface, in the ventricular cavity, and in the ventricular myocardium, special electrodes were designed for each position. For the epicardial leads, cotton wick electrodes were used. Two types were designed. When only one point was recorded, the records were obtained by applying a small cotton pledget approximately four millimeters square to the epicardium. The cotton was attached to an insulated wire and soaked in saline prior to use (Figure 1B).

When two or more areas of the ventricular surface were explored simultaneously, a lucite plastic holder containing three wick electrodes was used (Figure 1A). Each wick was approximately 2.5 centimeters long and 0.75 centimeter in width. When this device was applied to the beating heart the length of each wick allowed contact to be maintained during each cardiac cycle.

For recording electrical activity in the ventricular cavity, an electrode-tipped catheter was inserted into the cavity, via the auricular appendage (Figure 2).

When it was necessary to record both epicardial and endocardial leads simultaneously, a caliper-like
Fig. 1.-Cotton Wick Electrodes.

A. Lucite wick electrode holder for synchronous epicardial electrograms.

B. Single wick electrode for single point epicardial electrogram recording.
Cotton Wick Electrodes
Fig. 2.—Electrode-Tipped Cardiac Catheter.

The location of the recording tip is designated by the arrow. The other markings are reference points.
Electrode Tipped Cardiac Catheter
device was utilized (Figure 3A). A cotton wick electrode was attached to one leg of the caliper for epicardial leads. An insulated copper wire electrode was attached to the opposite tine.

For intramural (myocardial) leads a silver "plunge" electrode was used (Figure 4). A fine (0.023) gauge pure silver wire, three to five centimeters in length, was insulated throughout with three coats of lacquer, except for the extreme tip, which formed the recording surface. The recording tip was formed by grinding it to a sharp point. The exposed silver was chlorinated by immersion in dilute hydrochloric acid and an electric current of three volts passed through it. The silver wire was soldered to a copper lead-in wire and the entire joint insulated with lacquer. Markings of a contrasting color lacquer were placed at two-millimeter intervals along the wire to indicate the depth of the recording tip when inserted into the myocardium. The wire was of sufficient strength to allow insertion into the myocardium without bending, if the necessary care was exercised.

When it was necessary to record bipolar leads, one of two methods was used. Separate cotton pledget electrodes were used when two isolated points were to be recorded. When it was necessary to record two very near points (differential bipolar leads), a special
Fig. 3- Caliper Electrodes.

A. Unipolar electrodes.

There are three wires attached to the leg of the electrode which was inserted into the ventricular cavity. The center wire was opposite the epicardial surface.

B. Bipolar electrodes.

This electrode was also used for unipolar recordings by using only one of each pair of the wires.

Note the hinged joint on the left of each electrode. This joint allowed contact to be maintained with the epicardial surface by moving with each cardiac cycle.
FIGURE 3

Caliper Electrodes
Fig. 4- Silver Plunge Electrode. The electrode is enlarged approximately one and one-half times normal size.
Silver Plunge Electrode
device was used. It consisted of two plastic rods attached so as to form a pair of calipers, similar to the one previously described (Figure 3B). To each of these rods a pair of copper wires were attached for the leads. For simultaneous endocardial and epicardial differential bipolar leads, cotton wicks were attached to the pair of wires on the epicardial surfaces, and the endocardial pair were insulated throughout, except at the tips.

**Method of Study of the Cardiac Action Potentials**

Standard, unipolar, chest leads and vectorcardiograms were recorded on all animals prior to direct exploration of the heart. The standard limb leads were leads I, II, and III, with the limb attachment in the conventional manner. Leads AVR, AVL, and AVF were recorded in the conventional manner.

The chest leads were modified to fit the chest of the sheep by a numbering system similar to that described by Hamlin and Hellerstein, on the dog. The location and identification of each electrode placement is shown in Figure 5. By the system shown, variations in chest size and shape had little effect when considering the position of the electrode in relation to the heart. Both German silver contact and needle electrodes were
Fig. 5- The Thoracic Leads of the Sheep.
Each circle indicates the point of application of an electrode.
Thoracic Leads

FIGURE 5
used for the chest leads. No difference could be seen between the two types.

Vectorcardiograms were obtained using the Wilson Equilateral Tetrahedral system described by Helm and utilized by Hamlin and Hellerstein on the dog. Both the tetrahedral and cube system was tried on animals. The tetrahedral system gave more consistent results without excessive variations due to respiratory movements. Furthermore, the cube system does not lend itself to animal vectorcardiography, because of the laterally compressed chest of animals as compared to man, for whom the system was developed.

The nomenclature as described for man is not easily applied to an animal that stands on its four limbs. For that reason, more descriptive terms were applied to the views of each of the three planes taken in vectorcardiography. The frontal plane for man is in reality a ventral view of the cardiac vectors when an animal is in a standing position. Therefore the term ventral plane will denote that plane in the text.

The sagittal plane of man, viewed from the right side, remains sagittal in the animal, with the exception that the plane must be rotated ninety degrees clockwise, to conform with the standing position of the animal. The term sagittal plane will be used in the text with the understanding that it is rotated ninety
degrees to the right when compared with that of man.

The horizontal plane of man is in reality an anterior (cephalic) view of the cardiac vectors in the animal when viewed in a standing position. Therefore, the term anterior plane will be used in the text for this projection of the cardiac vectors.

Electrode Attachment for Vectorcardiography

The anterior plane was obtained by attaching the X axis electrodes to the right and left forelimbs with the left limb positive in relation to the right. The Y axis was obtained by attaching an electrode dorsal to the spinous process of the seventh thoracic vertebra and its mate to the central terminal of Wilson, with the exploring electrode negative in respect to the central terminal of Wilson (Figure 6).

The sagittal plane was obtained by utilizing AVF as the X axis, with that electrode negative in respect to the central terminal of Wilson. The Y axis was obtained by using the back point (LV 10), and the central terminal of Wilson. The back point electrode was negative in respect to the central terminal of Wilson (Figure 6).

The ventral plane was obtained by attaching the X axis electrodes to the right forelimb and left forelimb, with the left forelimb positive in respect to the right. The Y axis was obtained by utilizing AVF with
Fig. 6- Electrode Attachment for Vectorcardiography. The polarity of the lateral attachments has been rotated ninety degrees clockwise from standard terminology.
Technique for Vectorcardiogram
that electrode positive in relation to the central terminal of Wilson (Figure 6).

Direct Exploration of the Heart

With proper anesthesia, the chest was opened on the left side by a rib resection of the fifth and/or sixth rib. The costochondral junctions of the fourth, seventh, eighth, and ninth ribs were severed and retractors used to provide adequate exposure. Upon opening the thoracic cavity, artificial respiration was instituted and maintained throughout the entire study.

To expose the heart for exploring the entire surface of the left ventricle, an incision was made in the pericardium from the base to the apex. The edges of the pericardium were sutured to the surrounding external tissue, thus forming a hammock-like structure for the heart to lie within. With the heart so exposed, epicardial and endocardial exploration could be undertaken. It was necessary continually to apply warm saline to the surface of the heart to keep it from becoming dry.

When plunge electrodes were used, small windows, roughly one centimeter in diameter, were cut in the pericardium over the ventricular area to be explored. The electrodes were inserted through these windows into the myocardium, or completely into the ventricular cavity.
Epicardial Exploration

The epicardium of the left ventricle was explored using both the unipolar, bipolar and differential bipolar techniques. The entire surface of the left ventricle was divided into twelve areas (Figure 7). Each of these areas were recorded individually and/or simultaneously with one or two other areas, utilizing the cotton wick electrodes previously described.

In some instances electrograms of different sites on the surface of the left ventricle were recorded synchronously with a standard limb lead. This synchronous recording permitted timing of the onset of the intrinsic deflection at each of the sites. The nadir of the Q wave in the standard limb lead was used as a reference point for the timing studies because it was sharp and always occurred before or at the same time as the onset of the intrinsic deflection. Measurements were made at three different points, the onset, middle, and end of the intrinsic deflections. These were compared with the reference electrode.

Endocardial (Cavity) Exploration

Unipolar cavity potentials were recorded through the use of an electrode-tipped cardiac catheter, plastic rod electrode, or a plunge electrode. The records ob-
Fig. 7- The Areas of the Left Ventricle Used for Epicardial Exploration.
tained were essentially the same, whichever electrode was used. The cardiac catheter was inserted into the ventricular cavity via the left auricle. A small opening was made in the left auricular appendage with a sharp scissors. The catheter was inserted through this opening and threaded into the ventricular cavity, through the atrio-ventricular opening. A ligature around the appendage opening prevented the escape of blood. The electrode catheter was pushed into the apical region and slowly withdrawn. Recordings were made at various levels. The location of the recording tip could be roughly determined by observation of the markings on the catheter (Figure 2).

The plastic electrode was always used in conjunction with simultaneous epicardial and endocardial leads and will be discussed under that section.

**Simultaneous Epicardial and Endocardial Exploration**

To determine the time relationship between activation of the epicardium and the endocardium, it was necessary to record the two points simultaneously. It was also necessary to be assured that the points were both approximately at right angles to the ventricular myocardium and at approximately the same level. This was accomplished by using the caliper electrodes, or
a plunge electrode combines with a cotton wick electrode.

When using caliper electrodes, one leg of the caliper was inserted into the ventricular cavity. The other leg followed outside on the epicardial surface (Figure 8).

Both unipolar and differential bipolar leads were recorded at various levels from apex to base by sliding the caliper electrodes to various points and making recordings. Continual recordings were made by sliding the electrodes from the apex to the base while the recording machine was in operation. All areas that were capable of being reached with the apparatus were recorded.

Vectorgrams

The term vectorgram refers to a modified vectorcardiogram technique in which the electrodes are not attached to distant points, but attached to the pericardium. This technique was used to eliminate the possibility that the anatomical position of the heart in relation to the rest of the body would not influence the recording of the mean spatial vector forces of the heart.

The electrodes used were small cadmium-plated alligator clips attached to lead-in wires. The clips were lacquer insulated, with the exception of the teeth.
This method was used to obtain synchronous unipolar, bipolar and transmural records.
Technique of Synchronous Recording
on the very tip. Such clips were used because of the ease with which they could be attached to the pericardium. The attachment of the electrodes for each plane was as follows.

**Lateral plane** (similar to sagittal of the vectorcardiogram, viewed from the left side):

For the Y axis, one electrode was attached to the pericardium in the region of the apex of the heart, and the other at the base of the heart near the point where the pulmonary artery and the aorta are in apposition to each other. The polarity was so arranged that the one attached to the apex was positive in relation to the base electrode. On the X axis, one electrode was attached to the pericardium on its anterior surface, midway between the apex and the base. The other electrode was attached to the posterior surface of the pericardium midway between the apex and base. The polarity was so arranged that the electrode attached to the posterior surface of the pericardium was positive in relation to the other (Figure 9).

**Anterior plane** (similar to anterior plane of vectorcardiogram):

For the Y axis, the electrodes were attached the same as for the lateral plane. The positive electrode was on the apex and its mate—at the base.
Fig. 9 - The Technique for Obtaining Vectorgrams.
Technique for Vectorgram

Anterior Plane

Amplification System

Oscilloscope

Left Lateral Plane

Amplification System

Oscilloscope

Apical Plane

Amplification System

Oscilloscope
For the X axis, one electrode was attached to the right lateral portion of the pericardium, one-half way between the apex and the base, and the other electrode was attached to the left lateral pericardium in the same area as the one on the right. The polarity was so arranged that the electrode attached to the left side was positive in relation to the right one (Figure 9).

Apical plane (similar to ventral plane of vectorcardiogram):

The Y axis was obtained by attaching electrodes on the right and left lateral surfaces, similar to the attachments for the X axis of the anterior plane. The positive electrode was attached to the left side. The X axis attachments were obtained by attaching the electrodes on the anterior and posterior surfaces of the pericardium, similar to the X axis attachment of the lateral plane, with the positive electrode on the left side (Figure 9).

Intramural Exploration

In the study of intramural leads, it was necessary to establish a reference point for timing purposes. This was accomplished by the insertion of a plunge electrode through the free wall of the ventricle into the cavity, where it remained throughout the experiment.
This lead was recorded simultaneously with each intramural lead and with epicardial leads when taken. The nadir of the deflection served as a reference point for the timing of the intrinsic deflection of the epicardial and intramural leads.

Surface leads were taken through the pericardial windows over the free wall of the ventricle. After recording surface leads, plunge electrodes were thrust into the ventricular myocardium, at right angles to the epicardium, until the tip was in the ventricular cavity. The point of entrance into the cavity could be determined by observation of recordings made during its passage through the myocardium. As soon as the ST segment elevation disappeared, the cavity was reached. The electrode was then withdrawn in steps of approximately two to four millimeters. Intramural tracings were made at each level periodically for several minutes, until currents of injury became minimal. It was necessary for the electrode to remain at each particular level for approximately twenty to thirty minutes before the current of injury subsided. Since the ventricular wall of the sheep heart is approximately 15 millimeters thick, it was possible to make three to five recordings of the myocardium. Special attempts were made to record the sub-endocardial, the mid-point, and the sub-epicardial areas. After the experiment was concluded, the heart
Anatomical Studies of the Purkinje System

Since the Purkinje system is considered the functional structure for conduction of the cardiac impulse, attempts to outline clearly that system in the sheep and dog were made, using the technique described by Abramson et al. The Purkinje network in the sheep was outlined by injection of diluted India ink into the connective tissue sheath around the Purkinje fibers. The India ink could be visualized within the sheath, thereby enabling one to trace the network throughout the musculature. India ink was diluted nine to one with distilled water. This solution was drawn into a two-cc syringe, to which a 30 gauge one-eighth inch needle was attached. The point of the needle was carefully inserted into a visible portion of the Purkinje system, in a heart which had been opened by incising the ventricle between the two papillary muscles, from base to apex. Pressure was exerted until the ink could be seen to travel for a short distance through the network. The ink would spread for only a few millimeters. It was necessary to make several injections in order to visualize the system satisfactorily. Attempts to inject the dog Purkinje
Anatomical Studies of the Heart In Situ

In order to determine the exact location of the heart in relation to the exploring electrodes of the standard limb leads, chest leads and vectorcardiographic leads, studies of the heart in situ were made. This was undertaken to assure that the discrepancy between the dog and sheep electrocardiograms was not due to anatomical position.

Euthanasia was performed with an overdose of pentobarbital sodium. Records were obtained prior to death. A small opening was made in the rumen of the sheep, through which cresol solution was introduced into the rumen to prevent the formation of gas. The formation of gas would have forced the diaphragm forward, displacing the heart abnormally. The animals were placed in a freezer, at a temperature of minus 10 degrees Centigrade, in a right lateral recumbent position. In about 72 hours the body was frozen solid. Using an electric meat saw, the chest was removed from the rest of the body and sawed in three different planes through the middle of the heart as much as possible. The planes corresponded to the vectorcardiographic planes, i.e., saggital, ventral, and anterior. Photographs were taken of each plane.
EXPERIMENTAL RESULTS

The Standard Limb Leads

The configuration of the QRS complex in lead I fell into one of four categories: negative, diphasic, positive, or bizarre. Of the sheep examined, the majority were of the negative classification. Nine were negative, one diphasic, two positive, and four bizarre complexes were recorded.

The configuration of lead II was predominantly negative. Eight were negative, four diphasic, one positive, and three bizarre.

The configuration of lead III was almost equally divided among the categories. Five were negative, four were positive, four were diphasic, and three were bizarre.

In all except one animal, the voltages were low, rarely exceeding one-half millivolt.

Unipolar Limb Leads

The unipolar limb leads were somewhat more consistent in the appearance of the QRS configuration. Lead AVR was predominantly a positive deflection. Fourteen were positive, one negative of a low voltage, and one bizarre. Lead AVL was more divided as to configuration
with the majority falling in the negative classification. Eight were negative, five positive, two diphasic, and two bizarre. In lead AVF, the predominant deflections were negative and diphasic. Seven were negative, five diphasic, three bizarre, and two positive.

The voltages in the unipolar limb leads were more definitive than in the standard limb leads. However, the maximum voltage was, with the exception of one animal, less than one millivolt.

Typical standard and unipolar limb leads of the sheep are shown in Figure 10.

Chest Leads

The configuration of the chest leads was much more consistent than the standard limb leads (Figure 11). Lead LV 1 was remarkably consistent; all the deflections except one were strongly negative. The exception was diphasic.

Lead LV 3 was also remarkably consistent. It was the same as LV 1.

Lead LV 5 was near the transition zone. Seven records were negative, two positive and two bizarre.

Lead LV 7 was past the transition zone. The predominant deflection of this lead was positive. Ten were positive, three diphasic and two bizarre.

Lead LV 10 was the most consistent of all the
Fig. 10- The Standard and Unipolar Limb Leads of the Sheep. Each vertical line represents 0.04 of a second. The paper speed was 75 millimeters per second, three times normal speed.
FIGURE 10

Standard & Unipolar Leads

AVR

AVL

II

III

AVF

Standardization 1 mv
Fig. 11- The Chest Leads of the Sheep.  
Each vertical line represents 0.04 of a second. The paper speed was 75 millimeters per second, three times normal speed.
FIGURE 11
Chest Leads

Standardization 1mv
leads. All the deflections were positive.

Lead RV 3 was near the transition zone with eight diphasic, six negative and one positive deflection registered.

Lead RV 5 was predominantly positive. Ten were positive, one negative and one bizarre.

Lead RV 7 was positive in all but one, which was of negative character and of low voltage.

Vectorcardiograms

Vectorcardiograms made with an oscillograph are described as to the manner in which the loop is inscribed and to the direction of the vectors, as determined by observation of permanent records on photographic film. A composite of all the types of vectorcardiograms recorded is shown in Figures 12 and 13. An example of a typical vectorcardiogram of each plane of the dog is shown in Figure 14 for comparison with those of the sheep. There were only two QRS vectors found in sheep. The first, a small one directed toward the apex of the heart, was designated Vector A. This vector was not always present. The second QRS vector was large and consistently found. It was directed from the apex toward the base. The designation Vector B was given to this portion of the vector loop. It represents the mean vector force.
Figs. 12 and 13- Vectorcardiograms of the Sheep. Each figure shows the three planes for each of six sheep. The standardization was 1 millivolt equals three inches.
Vectorcardiogram

Ventral (Frontal)

Sagittal (Rotated 90° from standard)

Anterior (Horizontal)
Vectorcardiogram

Ventral (Frontal)

Sagittal (Rotated 90° from standard)

Anterior (Horizontal)
Fig. 14- Vectorcardiograms of the Dog. The arrow indicates the direction in which the loop was inscribed.
FIGURE 14

Standardization 1 mv

Sagittal

Ventral (Frontal)

Anterior (Horizontal)

The Vectorcardiograms of The Dog
Ventral Plane: The vector loop in the ventral plane was inscribed in both the clockwise and counterclockwise directions. Some reversed direction and were of figure-of-eight or bizarre type. Seven were inscribed in the clockwise direction, four in the counterclockwise direction and three were bizarre.

The mean spatial vector force, Vector B, was more commonly directed anterior and to the right. Ten recordings were directed to the right and four to the left. Twelve were directed anteriorly and two posteriorly. Of the two posterior ones, neither were strongly posterior, but were somewhat bizarre, with the major component directed posterior.

Sagittal Plane: The majority of the records obtained on the sagittal plane were inscribed on a counterclockwise manner. Eight were inscribed in a counterclockwise direction, four in a clockwise direction, and two were bizarre.

An outstanding fact was noted in the mean direction. All of the animals examined showed a mean vector force directed dorsally on the sagittal plane. Almost all of the force was directed anteriorly. Eleven records showed anterior direction with three slightly posterior.

Anterior Plane: All of the records obtained in the mean vector force.
anterior plane were inscribed in a clockwise direction with the exception of three which are so bizarre as to prevent determination of the manner in which the loop was inscribed. The major vector force in all of the measurable records was directed anteriorly. Ten were directed to the right and four to the left.

Unipolar Epicardial Electrograms

A composite of the unipolar epicardial electrograms of one typical animal is shown in Figure 15. A typical epicardial electrogram of the dog is shown in Figure 16 for comparison purposes.

Area 1 of the unipolar epicardial electrograms was variable in the configuration of the QRS complex. There were five Rs, two rS and one qR complexes registered in this area.

Area 2 was consistently a negative deflection. Five complexes were QS and two rS, with the r extremely small compared to the S wave.

Area 3 was consistently negative, with the exception of one animal. Five complexes were rS, one QS, and one positive of the Rs type.

Area 4 was similar to area 1. Four complexes were of the qRS type, three rS and two qR.

Area 5 was exceptionally consistent. All of the deflections were strongly negative, of the QS con-
Fig. 15- Unipolar Epicardial Electrograms of the Sheep. The position of the record designates the area from which it was obtained.
FIGURE 15

Unipolar Epicardial Electrograms

↓ Denotes Standardization 1 mv.
Fig. 16- Unipolar Epicardial Electrograms of the Dog. The position of the record designates the area from which it was obtained.
Unipolar Epicardial Electrogram of Dog
Area 6 was also negative, with the exception of one diphasic deflection. Six were QS, four Rs, and one diphasic RS deflection.

Area 7 was similar to areas 1 and 4. Three deflections were QS, five qRs, and three bizarre.

Area 8 was consistently negative, with the exception of two animals. Five were QS, three Rs, one diphasic of the Rs type, and one qRs.

Area 9 was consistently negative, with the exception of one diphasic deflection. Eight were Rs, one QS, and one diphasic of the RS type.

Area 10, like areas 1, 4, and 7, was variable, with more positive deflections than negative. Five were qR, two bizarre, two qRs and one diphasic RS.

Area 11 was consistently negative. Six were of the Rs type and four of the QS type.

Area 12 was consistently negative. Five QS and five Rs deflections were recorded.

Areas 1, 4, 7, and 10 were near the base of the heart. Almost all deflections from these areas were positive.

Areas 2, 5, 8, and 11 were in the middle of the left ventricle. The majority of the leads were strongly negative, with only two exceptions. One was diphasic of the RS type and the other a qRS.
Areas 3, 6, 9, and 12 were near the apex of the heart. All the deflections recorded in these areas were strongly negative, with the exception of two di-phasic QR complexes.

It can be stated that all of the epicardial surface, with the exception of the area immediately adjacent to the coronary groove, is electronegative when explored with a unipolar electrode.

The Time Relationship Between the Different Areas of the Epicardial Surface

The results of the time measurements between a reference electrode and the direct electrogram are shown in Figure 17.

At the apex of the left ventricle and the free wall, the onset of the intrinsic deflection appeared synchronous with the nadir of the Q wave (time zero) of the reference electrode.

The anterior wall deflection occurred next in the sequence by approximately 10 milliseconds, followed by the posterior wall in 15 milliseconds from time zero. On one recording the base of the middle free wall occurred at the same time as the posterior wall. The base of the anterior and posterior walls occurred last on an average of 25 milliseconds from time zero.
Fig. 17- The Time of Activation of the Epicardial Surface of the Sheep's Heart. Each area has a set of three numbers differentiated by gradation of shade. The black (upper) indicates measurements obtained at the onset of the intrinsic deflection. The dark crossed numbers (middle) indicate measurements obtained at the end of the intrinsic deflection. The lightest (bottom) indicates measurements made at a mid-point between the two previous measurements.
FIGURE 17

Time of Activation of Epicardial Surface
Bipolar Electrograms

Bipolar electrograms were used for timing purposes. The complexes recorded, using the bipolar differential technique, are bizarre when compared with unipolar electrograms. However, according to Lepeschkin, the sharp onset of the spike or most rapid deflection is used as the criterion for timing excitation at the point immediately under the exploring electrodes.

Bipolar leads were also made with the two electrodes situated far apart. These were used to determine the direction of the excitation wave in relation to the positive exploring electrode, an upward deflection denoting the wave approaching the positive electrode and a negative deflection denoting the wave receding from the positive exploring electrode.

Bipolar Transmural Leads: The types of deflections recorded consistently started with a Q wave. QR, qs, and Qr deflections were recorded (Figure 18).

Bipolar Apex to Base Leads: In all records taken using this technique, a large R wave was always recorded. The R was preceded by a small q and in one case the R was followed by a small s wave (Figure 19).

Bipolar Differential Apex to Base Leads: When measure-
Fig. 18- Bipolar Transmural Lead. The positive electrode is located on the endocardial surface, the negative on the epicardial.
FIGURE 18

Bipolar Transmural
Fig. 19- Bipolar Electrogram Apex-Base. The positive electrode is located on the base of the heart, the negative on the apex. Paper speed was 50 millimeters per second. Each vertical line represents 0.02 of a second.
Fig. 20- Bipolar Differential Apex-Base Leads. Paper speed was 50 millimeters per second. Each vertical line represents 0.02 of a second.
Two Differential Bipolar-Synchronous Recording
ments were made relative to time, the difference in time from apex to base was approximately ten milliseconds. (Figure 20).

**Bipolar Differential, Epicardial and Endocardial:** The results revealed three areas of time differential: apical, free wall, and basilar region. In the apical region the time differential was approximately 10 milliseconds. The free wall differential frequently was immeasurable. When it was possible, no more than 3 milliseconds could be measured. In the basilar region a 10 to 15 millisecond difference was measured. In all cases, the endocardial lead occurred first, with the exception of the free wall, where no time difference was noted (Figure 21).

**Simultaneous Unipolar Electrograms**

**Simultaneous Epicardial and Endocardial Electrograms:** The onset of the intrinsic deflection occurred almost simultaneously in the epicardial and endocardial leads from the free wall of the left ventricle. The deflections were QS in the cavity and rS or QS on the epicardium.

In the apical region a time difference could be measured in some animals. A difference of approximately 8 to 10 milliseconds endocardial to epicardial was
Fig. 21- Synchronous Bipolar Differential Epicardial-Endocardial Records. Each pair of the three areas shown was recorded synchronously.
FIGURE 21

Synchronous Bipolar Differential
measured. In the basilar region an Rs or qRs deflection was obtained from both endocardium and epicardium. A time differential between the endocardium and epicardium of 10 to 15 milliseconds was measured. The endocardium occurred first (Figure 22).

Vectorgrams

The configuration of the vectorgrams of the four sheep on which the technique was used did not fall into a specific pattern. However, all were roughly arrowhead shaped (Figure 23).

The left lateral view, which corresponds to a left lateral (sagittal) vectorcardiogram, was inscribed in a clockwise direction with the exception of one which was a figure-of-eight type.

The anterior view, comparable to the anterior (horizontal) vectorcardiogram, was inscribed in a counterclockwise direction on two animals and a figure-of-eight in the remaining two.

The apical view, comparable to the ventral (frontal) plane of the vectorcardiogram was inscribed in a clockwise direction with the exception of one which was bizarre.

The major vectors of the spatial QRS vectorgram consisted of two vectors designated A and B (A-apex and B-base).
Fig. 22- Synchronous Unipolar Epicardial-Endocardial Records. Each pair of the five areas shown was recorded synchronously.
FIGURE 22

Synchronous Unipolar
Fig. 23 - Vectorgrams of the Sheep Heart. Each record was inscribed in a clockwise direction. The arrow indicates the direction of the mean spatial vector of the QRS complex.
Vectorograms

Left Lateral

Anterior

Apical
Vector A, a small vector, was directed toward the apex and toward the right. Vector B, the largest of the vectors, was directed toward the base and to the right. There is no third vector as found in the dog and man.

Myocardial Unipolar Electrograms

Recordings made in the free wall of the left ventricle 2 millimeters in the subendocardium were rS or QS deflections. Leads taken in the middle of the myocardium and at all points from the subendocardium to the middle were QS or rS deflections. Subepicardial and epicardial leads were QS deflections. Occasionally a small embryonic r wave was seen on the epicardium. This is in contrast to that found in the dog. In the dog a QS deflection is seen in the myocardial layer from the endocardium out to approximately two-thirds of the myocardium, where the recordings abruptly change to an RS and then to an Rs type on the epicardium (Figure 24).

The time relationship of the occurrence of the intrinsic deflection at various levels of the myocardium were remarkably small in the sheep. It was almost impossible to detect any difference in time between the electrode points. This result is in contrast with the observation dog. In the inner one-half to two-thirds
Fig. 24 - Myocardial Unipolar Electrograms of the Sheep and Dog. Each point of the myocardial lead was recorded synchronously with a reference electrode for timing purposes. The small circle indicates the reference electrode.
FIGURE 24

Intramural Unipolar Electrograms

Dog

Sheep

Endocardium

Epicardium

Cavity Electrode (Reference)
of the myocardium of the dog, the time relationship be-
tween points is extremely small, but in the outer one-
half to one-third there is a definite indication of
slow activation of the myocardium.

Another exceptional finding was noted when a com-
parison of the duration of the intramural ventricular
complex between the sheep and dog is made. The duration
for the sheep is approximately 25 milliseconds, whereas
for the dog it is at least 40 milliseconds.

Anatomical Studies of the Purkinje System

The Purkinje system as outlined by the technique
previously described, demonstrated an atrioventricular
node with a short bundle of His and two bundle branches,
the right and the left. The left bundle branch is de-
rived from the common bundle at the base of the septum
and follows a subendocardial route down to approximately
two centimeters above the two large moderator bands.
At this point it branches, sending a large portion of
its fibers to each of the moderator bands, and a small
portion to the remainder of the septum toward the apex.
The fibers located upon and within the two moderator
bands can be seen very clearly (Figure 25). They tra-
verse the ventricular cavity from the septum across to
the base of each papillary muscle. Upon reaching
Fig. 25- The Purkinje System of the Ovine Heart.
Left Bundle Branch
Moderator Bands with Purkinje Fibers
Subendocardial Purkinje Fibers

Purkinje System of Ovine Heart
the papillary muscle, they branch extensively, uniting and rebranching to extend throughout the subendocardium of the free wall of the left ventricle, with the exception of the base. The base appears to have little or no Purkinje network.

From the subendocardial network, myocardial fibers penetrate the musculature of the wall of the ventricle.  

According to Abramson, the myocardial Purkinje fibers of the sheep penetrate the muscle substance as far as the epicardial surface, forming plexuses which extend obliquely or roughly parallel to the subendocardial Purkinje network.

The Purkinje fibers of the dog were impossible to differentiate by the injection technique. There were no fibers seen crossing the ventricular cavity via moderator bands. According to Abramson, the size of the Purkinje fiber in the dog is smaller than that of the sheep and lacks the connective tissue sheath. The myocardial network is small and does not extend to the epicardium.

**Anatomical Studies of the Heart In Situ**

The cross section of the frozen thorax revealed that the heart lies in an almost vertical position. The apex of the left ventricle lies on the inner surface of the sternum. The base faces almost directly
dorsal. The plane of the interventricular septum lies on the minus 80 degrees plus 100 axis of the sagittal plane cross section, and minus 45 degrees plus 135 degrees axis on the ventral plane. Thus the left side of the interventricular septum faces posterior and left. The free wall of the left ventricle is located caudal, to the left, and parallel to the interventricular septum. Photographs of the position of the heart correlated with a vectorcardiogram are shown in Figure 26.
Fig. 26- Anatomical Position of the Ovine Heart In Situ Correlated with Vectorcardiograms. The ventral section was cut two inches above the level of the costochondral junction. The sagittal section was cut on the median plane. The anterior section was cut at the level of the seventh thoracic vertebra.
Correlation of V.C.G. with Anatomical Positions in Sheep
DISCUSSION

In this study it is assumed, as in other studies, that the electrical phenomenon recorded by all except direct leads from the heart itself, represents the summation of depolarization potentials occurring in the muscular mass of the ventricles. The recordings obtained are a result of the cancelling forces and the summing forces occurring simultaneously.

Standard Limb Leads

The voltages recorded on the standard limb leads are remarkably low for the size of the heart when compared to the dog and man. When diphasic or low voltages of either negative or positive type are recorded, it is accepted by electrocardiographers that the mean spatial vector force is directed at right angles, or nearly so, to the exploring electrodes. Observation of the vectorcardiograms, vectorgrams and anatomical studies indicate that the mean spatial QRS vector is directed at approximately right angles to the exploring electrodes used in the standard limb leads. This fact would account for the difficulty encountered by early investigators in interpreting electrocardiograms taken
of ruminants by the standard leads used on man.

The Chest Leads

The chest leads were much more consistent than the standard limb leads. Negative deflections were always recorded in the region of the apex of the heart. A transition zone was at right angles to the anatomical base of the ventricles. Positive deflections were always recorded above this plane.

Vectorcardiograms, vectorgrams and anatomical relationship studies indicate that the large mean spatial vector force (Vector B) is directed away from the apex toward the base of the heart. Vector A is occasionally seen as a small r in the chest leads below the transition zone. This vector can be assumed to be due to activation of the interventricular septum, occurring in a tangential manner from base to apex and slightly toward the right or left.

Vector B is directed away from the apex toward the base and to the right or left. This is demonstrated in the scalar chest electrocardiograms. Leads LV 1, LV 3, and RV 3 were strongly negative. Leads above this point became progressively positive, indicating that Vector B was directed from the apex to the base.

The voltages recorded on the chest leads were larger than those found in the standard limb leads.
However, they are less than the voltages found in dog and man. The low voltages can be attributed to excess fat surrounding the heart and disease conditions. Most of the animals used in this experiment were not excessively fat nor were they diseased. Another factor which may be associated with low voltages is the cancellation forces of other depolarization processes taking place simultaneously and directed opposite to the ones in question. This is a distinct possibility in the sheep heart when one considers the arrangement of the Purkinje system ramifications. It is possible that the apical portions of the interventricular septum, the apical portion of the left ventricle and the lateral wall of the left ventricle, below the papillary muscles, are activated almost simultaneously. Kisch found in the calf that the occurrence of the intrinsic deflection of the apex of both ventricles and the ventral lateral wall did occur at the same time. Recordings in this study were the same as those found by Kisch.

Vectorcardiograms

Ventral (Frontal) Plane: In the ventral plane the vectorcardiogram indicated that Vector A is not demonstrable to any extent, since most of it is travelling at right angles to the plane recorded. Therefore, the depolarization process of the interventricular septum,
apical region of the ventricles, and ventral portion of the free wall is recorded poorly, or not at all.

Vector B, which represents the activation process of the remainder of the ventricular mass, is demonstrated on this plane. It is directed anteriorly and to the right or left. The activation apparently progressed through the free wall from each papillary muscle tangentially toward the base. It occurs almost simultaneously in the posterior and anterior wall.

**Sagittal Plane:** The activation process responsible for Vector A could be visualized in most of the records on the sagittal plane. It indicated that the depolarization process was directed ventrally either anteriorly (most common), posteriorly, or strictly ventral. Vector B was directed dorsally and anterior. This force represented the activation of the lateral wall and base of the ventricles. The records would indicate that the activation process was moving in a tangential manner toward the base of the heart.

**Anterior (Horizontal) Plane:** The A vector could be visualized frequently in the anterior plane. In all but two animals it was directed toward the right, indicating that the early septal activation proceeded from left to right at a small angle. B vector was always directed dorsally in this plane, indicating that the main muscle
mass of the left ventricle was activated toward the dorsum of the animal.

The Spatial Vectors

This study indicated that there are two spatial vectors in the ovine vectorcardiogram. These vectors indicate the depolarization process as it progresses through the ventricle, and are related to the activation of specific anatomic structures. The first vector designated Vector A is directed ventral, slightly to the right or left and either anterior or posterior to a small degree. This vector represents activation of the interventricular septum and a portion of the apical region of the ventricles.

The second vector, designated Vector B, the larger of the two, is directed anterior, dorsal and to the right or left. This vector represents activation of the lateral, anterior and posterior wall and the base of the heart. The fact that the vector is directed in the same direction as the anatomical long axis of the heart indicates that the mean activation of the musculature must occur in a tangential manner toward the base.
Vectorgrams

To be sure that the recordings made were in true relationship with the anatomical position of the heart the vectorgrams were made. Correlation between the vectorgrams and the vectorcardiograms was good. The vector forces seen in the vectorcardiograms were present in the vectorgrams in approximately the same proportion and direction.

Electrograms

It is generally accepted that in direct unipolar leads a positive deflection is caused by activation processes approaching the electrode through the muscle not in contact with it. This is called the extrinsic deflection. As soon as the activation processes reach the ventricular surface under the direct electrode, the potential suddenly changes to negative, as it now lies on the negative side of the activation process. This negative deflection is called the intrinsic deflection. The onset of the intrinsic deflection or the steepest portion indicates the moment when the center of the excitation front has reached the epicardial surface directly under the electrode (Lepeschkin).

The surface of the sheep's heart can be roughly divided into three electrogram zones: (1) the apical
region upward for about four centimeters, (2) the an-
terior, posterior, and free wall of the ventricle, up
to within three centimeters of the base, and (3) the
basilar region, approximately three centimeters wide.
The first zone had a small r wave followed by a large
Q. This would indicate an oncoming activation process
followed by a receding one of greater magnitude. Anato-
merically the electrode faced the interventricular
septum and the apical region of the ventricle. The r
wave recorded can be attributed to a summation of the
forces generated in those structures. The large Q
wave can be attributed to the receding activation
occurring in the remainder of the muscular mass.

The second zone was strictly a deep QS deflection.
This indicates practically no front approaching the
exploring electrode. This is most surprising since
it is generally considered that activation proceeds
from the endocardium toward the epicardium. There are
two possible reasons why a QS was recorded in this zone.
Either the activation front was proceeding in the oppo-
site direction to the generally accepted concepts in
other mammals, such as the man or the dog; or depolar-
ization was occurring almost instantaneously throughout
this region and the exploring electrode only faced the
negative side of the activation process. If the activa-
tion front was directed from the epicardium toward the
endocardium, positive deflections should be recorded on the endocardium and in the ventricular cavity. Also, there should be a time differential between the epicardium and the endocardium with the epicardial activation occurring first. This was not true, as will be discussed later. Instantaneous activation of the muscular mass of this region will be discussed in the section on intramural leads. The third zone, a semicircular area around the base revealed qRs or Rs deflections. The first negative deflection when recorded can be considered an extrinsic deflection due to activation of the septum. The q occurred more frequently when the exploring electrode was near the interventricular septum. The large R deflection indicates an activation front of considerable magnitude approaching the exploring electrode. The small s indicates the passage of the activation front, and a small receding front of low magnitude. The depolarization of zone two could account for the large R wave, and small s could be caused by small areas of the base being activated slightly later than that under the exploring electrode. Anatomical studies of this region reveal a lack of Purkinje fibers. This lack of conduction network may contribute to the configuration of the leads taken in this region.
The Time Relationship Between the Different Areas of the Epicardial Surface

In time relationship studies between the different areas of the epicardial surface, the sequence of the start of the intrinsic deflections was found to be: apex and lower lateral wall—anteri or wall middle—posterior wall middle—middle base of the anterior and posterior wall—base of the anterior and posterior wall. (Figure 17). This would indicate that activation of the apical region and the lower portion of the free wall occurs early. Therefore cancellation forces of the apex and middle free wall could occur. The early occurrence of the excitation of the lateral free wall could be based on the presence of the large number of Purkinje fibers which cross the ventricular cavity via the moderator bands. The area so supplied with the conduction network would be activated at the same time, or nearly so, as the apical region. The distance from the point of divergence of Purkinje fibers, from the main bundle to each area, is approximately the same. The small r wave recorded probably is a net result of the cancellation and summation forces.

The anterior, followed by the posterior wall, plus the later activation of the base would account for the large Q waves recorded, except near the base. The large R waves recorded at the base could be a result
of the sum of activation processes from the regions below, and the muscle fiber to muscle fiber conduction which may occur in this region because of the lack of conduction network.

It would appear that the spread of excitation was spreading in a complex tangential manner in the anterior and posterior wall, then to the base. The mean force generated would be directed from the apex toward the base. This correlates with the finding noted in the vectorcardiograph, vectorgraphs, and vector analysis of the standard and chest leads.

Unipolar Endocardial Electrograms

Electrograms recorded from the cavity immediately adjacent to or on the endocardium were remarkably similar to the epicardial electrograms on the opposite side of the ventricular wall (Figure 23). The only exception was the lack of an r wave near the apex. The lack of this positive deflection can be accounted for by assuming that the activation processes were receding from the exploring electrode in the interventricular septum from left to right and that activation of the apical region was proceeding from the endocardium toward the epicardium in the outer layer. Since the deflection was strictly negative in the remainder of the cavity except near the base, the
activation front was not approaching the cavity from the epicardium. Simultaneously recorded epicardial and endocardial electrograms directly opposite each other were both negative deflections and occurred simultaneously (Figure 23). This would indicate that the depolarization process was occurring throughout the muscle mass instantaneously, or at such a rapid rate that no activation fronts were advancing toward either exploring electrode. Since it had been found that the Purkinje conduction system ramifies throughout the muscular mass of the ventricle, and that the speed of conduction through this system is 4000 to 6000 millimeters per second, it is entirely possible that because of the rapid rate of transmission, depolarization would begin almost simultaneously at the endings of many Purkinje fibers (Figure 27). Activation would occur at many diffusely scattered foci, thus the exploring electrodes would be located on the negative potential side in relation to the indifferent electrode.

Time Relationship Studies Between the Endocardium and Epicardium

Both unipolar and bipolar leads were used to time the onset of the intrinsic deflection. The results were essentially the same. The same three zones as described previously have time of activation relation-
Fig. 27- The Depolarization Process of the Left Ventricle of the Sheep and Dog. The arrows indicate areas of a true activation front.
Depolarization Process

Dog

Sheep
ships. In the apical region the endocardium was activated 8 to 10 milliseconds before the epicardium and early in the electrical cardiac cycle. This would produce a small activation front directed toward the apex. In the vectorcardiograms, vectorgrams, and the epicardial unipolar leads, a recording characteristic of an approaching front was found for this anatomical region.

In the large free wall zone, no time difference could be recorded between simultaneous epicardial and endocardial leads. This indicates that depolarization of the muscular mass of this region occurred almost instantaneously.

Recordings made in the basilar zone were distinct-ly different from the other zone. There was a time differential of approximately 15 to 20 milliseconds between the endocardium and the epicardium. The endocardium was activated first. This indicates that there is an activation front occurring in the basilar region, and was recorded as such. The speed of conduction in this area, 400 to 500 millimeters per second, is typical of muscle fiber to muscle fiber conduction. This can be correlated with the observed lack of conduction tissue of the area.
Intramural Time Relationship Studies

The results of the unipolar serial intramural leads recorded in the free wall of the left ventricle from epicardium to endocardium were all negative deflections. The intrinsic deflections occurred almost instantaneously. The time differential was almost impossible to measure. These recordings confirmed the assumption that the entire mass of the lateral wall was activated at multiple foci throughout the ventricular wall, and that it occurs within such a short interval of time that it is difficult to measure with the present equipment.

Studies of the dog's heart using plunge electrodes, 26, 27 by Prinzmetal et al. indicate that the depolarization process passes almost instantaneously through the inner layers and relatively slowly through the outer layers. The explanation of this rapid spread in the inner layers is based on the distribution of the Purkinje system. The system in the dog does not extend to the outer layer, but terminates in the mid-ventricular region. 26, 27

Prinzmetal concluded that because of the rapid rate of transmission in the Purkinje system, depolarization of the subendocardial musculature would begin almost simultaneously at the endings of many
Purkinje fibers. If this is true for the dog, then the entire myocardium of the sheep's heart is similar to the inner layer of the dog's heart. The records obtained indicate that such may be true.
SUMMARY

One objective of this investigation was to determine the exact mean spatial vector forces of the electrical activity of the ovine heart. It was necessary to establish this fact, since detailed vector analysis of the forces was lacking in the literature. It has been suggested, however, by Smith, Alfredson and Sykes, Lepeschkin, and Kisch that ungulates differ from other mammals in the activation process.

The second objective of the investigation was to determine the exact process of excitation of the left ventricle.

To reach these objectives, a series of experimental procedures was designed.

The first of the procedures consisted of examining the heart from a distance by utilizing the standard limb leads, chest leads, and vectorcardiograms. By analysis of the results obtained it was determined that the mean spatial vector forces of the sheep's heart consisted of two major vectors. The first force, termed Vector A, was directed posterior, slightly dorsal or ventral, and slightly to the right or left. It was the smaller of the two forces, with a ratio of approximately 1:5. The second and largest vector force, termed
Vector B, was directed anterior, dorsal, and to the right or left.

From the results of the records obtained, it was concluded that:

(1) The mean spatial vector forces of the ovine heart are different from those reported for the dog and man.

(2) It would be necessary to investigate the mechanism of spread of activation to determine the cause for the differences noted.

The second procedure consisted of examination of the heart directly, by opening the chest and applying electrodes directly to the heart.

Vectorgrams, a modified vectorcardiographic technique, directly from the pericardium revealed results similar to distance leads. This indicated that the anatomical position of the heart in the chest was not responsible for the differences noted in other animals by distance leads.

Epicardial electrograms revealed that the surface of the sheep's heart was electrically different from that of dog and man. The epicardial surface could be divided into three zones: (1) apical, (2) anterior, free, and posterior wall, and (3) basilar. The first zone yielded RS type deflections, the second primarily QS deflections, and the third Rs deflections.
These results indicated that the epicardial surface, with the exception of the base, faced the electronegative portion of the activation process. Two possible reasons for electronegative deflections were suggested:

(1) That the activation front proceeded from the epicardium toward the endocardium. This is contrary to the accepted pattern of spread.

(2) That activation of the entire musculature occurred synchronously, thus placing the exploring electrode on the negative side of the depolarization process in respect to the rest of the body.

Endocardial electrograms using special design equipment were made. The results obtained were surprisingly similar to the epicardial leads. One exception was noted. The small r wave noted on the epicardial leads in the apical region was absent. The results disprove the suggestion that the spread of activation was from the epicardium toward the endocardium. There remained the possibility that activation was synchronous throughout the muscular wall.

Simultaneous endocardial and epicardial electrograms revealed an exceptionally small time differential between the onset of the intrinsic deflection. This is in contrast with the results found by other investigators, and confirmed by the present one, on the dog's heart. The onset of the intrinsic deflection occurs
considerably sooner (15 milliseconds) on the endocardium than on the epicardium of the dog.

Intramural electrograms at approximately 2-millimeter intervals from epicardium to endocardium were made. Negative deflections were recorded throughout. This is in contrast with that found in dogs. In the dog, the QS deflections found in the inner layer convert to an Rs deflection. The conversion is abrupt at about the middle of the myocardium.

Time relationship studies of the intramural leads indicate that in the free wall of the ovine left ventricle, the onset of depolarization is almost synchronous throughout. In the dog, the onset of depolarization occurs synchronously in the inner layer but not in the outer layer. This gives rise to a comparatively slow activation front progressing from the mid-myocardium to epicardium.

Time relationship studies between different areas of the epicardial surface were investigated to determine the time of onset of the intrinsic deflection. Electrograms of different sites were recorded synchronously with a standard limb lead as a reference point. The results obtained showed that the following sequence of activation occurred: apex and lower lateral wall—middle of the anterior wall—middle of the posterior wall—base of the anterior and posterior wall.
It would appear from the results obtained that the spread of excitation was complex in the septal, apical and lateral free wall, yielding many cancellation forces. Activation then occurred in a complex, multifocal, tangential manner toward the base. Fewer cancellation forces occurred during this time.

All of the findings of the second group of experimental procedures suggest that there may be some anatomical basis for the records obtained. The distribution of the ovine Purkinje system is markedly different from that of the other extensively studied animal, viz. the dog. Anatomical studies show that the main bundle branch of the left side divides early on the upper portion of the septum into two trunks, which cross the ventricular cavity via the moderator bands to the base of each papillary muscle. Smaller trunks spread down the remainder of the septum and ramify early throughout the septal musculature. Upon reaching the papillary muscle base, the main trunks arborize rapidly and spread to the remainder of the ventricular walls. The base is devoid of Purkinje fibers.

The results of the last group of experiments and the anatomical studies suggest a mechanism of the excitation process based upon specific anatomical structures.

The spread of the excitation wave in the ovine
left ventricular myocardium may be as follows. The impulse from the common bundle spreads down the left bundle branch to the first arborization in the upper interventricular septum, where initiation of muscular activation occurs. Almost simultaneously, with the early septal activation, the impulse spreads across the ventricular cavity via the two moderator band trunks, to the base of the anterior and posterior papillary muscles. The extensive ramifications of the Purkinje system, from those points throughout the muscular wall to the epicardium, allow instantaneous multifocal depolarization to occur. The ventral portion of the free wall and the apical region would be activated at the same time as the remainder of the interventricular septum. Activation of the anterior, then posterior wall would follow, based upon conduction tissue distribution. The base would be activated last and progress in a true activation front due to the lack of conduction tissue in this region.

Records obtained from the surface of the animal's body correlate well with the proposed description of activation. Vector A corresponds to the septal, apical and ventral lateral free wall. Vector B corresponds to the activation of the anterior and posterior wall and the base of the heart.


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In 1946 I was called into active service as an officer in the Veterinary Corps, Army of the United States. Upon discharge from the service in 1948, I joined the staff of the College of Veterinary Medicine as an instructor in the Department of Veterinary Surgery, Ohio State University. I received the degree of Master of Science from this institution in 1950. The same year I accepted an assistant professorship of Small Animal Surgery with the University of California, Davis, California.

In 1951 I joined the clinical staff of the School of Veterinary Medicine, University of Georgia, Athens, Georgia, as Assistant Professor and Surgeon in Charge.

In 1953 I returned to the Ohio State University to complete the requirements for the degree of Doctor of Philosophy. While in residence I was employed as an Instructor in the Department of Veterinary Physiology and Pharmacology.