Activation of the Interventricular Septum

By ALLEN M. SCHER, PH.D., ALLAN C. YOUNG, PH.D., ARTHUR L. MALMGREN and ROBERT V. ERICKSON

Multipolar recording techniques have been used to study excitation of the canine interventricular septum. Activity commences in the mid left septal endocardium and slightly later near the right anterior papillary muscle. From these sites depolarization spreads over the endocardial surfaces, probably via the Purkinje tissue, at 1 m./sec. and through the septal thickness at one-third this speed. Near the upper septum, bilaterally and on the posterior right there is a lack of the rapid endocardial conduction. Septal contribution to the QRS is considered.

ACCORDING to common belief, the interventricular septum is excited from base to apex and from left to right. This pattern, as described by Lewis, is supposed to result from the branching of the left conducting bundle high on the septal wall while the impulse on the right is still confined within the bundle. Septal excitation has been considered to produce in this fashion the initial "Q" deflection of the electrocardiogram.

In their classical study of ventricular activation, Lewis and Rothchild found some points near the base of the septum which were excited later than points more apical, but neither they nor most later writers included such observations in their discussions of septal activity. Recently two groups of investigators, working independently under Burchell and Sodi-Pallares, published evidence that the apex of the septum is excited before the base, and that the left side is excited before the right. Using multichannel recording apparatus and procedures, we have examined the electrical invasion of the septum in detail.

METHOD

The multipolar electrode, the 16-channel oscilloscope and other techniques used have previously been described in detail. The electrode consists of fifteen fine wires assembled around a central shaft. The cut ends which are used to record are 1 mm. apart. The maximum diameter of the assembly is 0.3 mm. The pre-amplifiers used in this study have been newly designed. They feature input impedance of 109 ohms and overall frequency response from D.C. to over 40 kc. The oscilloscope has 16 tubes and a common sweep generator. Since the horizontal amplifiers may differ from one another, a time-pip at five milliseconds intervals is fed into all channels simultaneously from a master generator. A switch on the pre-amplifier chassis permits unipolar (each terminal against a distant point) and bipolar (difference between adjacent terminals) leads to be taken. Throughout an experiment one oscilloscope channel records a time reference from a fixed point in the heart and another, a Lead II ECG.

In early experiments, some electrodes were inserted from base to apex and vice-versa. For reasons which will later appear, it was found most profitable to insert the electrodes perpendicularly into the septum through the right wall and cavity. Successful experiments were carried out in this fashion in 25 dogs, three monkeys and one goat. Although some electrodes were 30 mm. long, it was almost always possible to insert electrodes 15 mm. long through the septum, so that the recording terminals near the tip were in the left cavity and those near the end, in the right cavity. Electrodes inserted in this fashion can be easily deflected or bent; therefore, electrode position was carefully checked, and no data in this study was derived from electrodes whose positions were not verified.

In many experiments, extrasystoles were elicited from various points on the septal electrodes, and the resultant patterns of excitation recorded on the stimulating and other electrodes.

Most of the experiments were plotted as in the accompanying figures. In some experiments, the measurements of the position of each electrode were used to construct exact three-dimensional models of the tissue, and colored beads were placed at each terminal to designate the times of local activation. Such models were extremely useful in visualizing the pattern of septal activation.

During two experiments, electrodes apparently pierced the right bundle producing the electrocardiographic pattern of bundle branch block. These experiments are not reported here.

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RESULTS

Fig. 1 indicates the position of an electrode inserted into the septum in one experiment. The tip of the electrode was in the left cavity and the recording terminals near the end were in the right cavity.

Fig. 2 shows potentials recorded along this insertion. The first two channels in the unipolar record on the left show the slow deflections characteristic of the cavity. These are from the left ventricular cavity. Records from the last three electrode positions (channels 12, 13 and 14) also show cavity potentials, in this case from the right. The irregularities in channel 12 indicate that the electrode was very close to muscle. The intervening channels (3 to 11) record potentials across the septum. A fixed time reference potential appears on channel 15 and a Lead II ECG, on channel 16. Time pips at five milliseconds intervals appear in all channels. The unipolar records indicate that depolarization (sharp negative deflection) occurs earlier near the endocardial surfaces than in the center of the septum. The left endocardial surface was excited earlier than the right along this electrode. The bipolar records on the right of figure 2 indicate the same progression. A downward (negative) deflection indicates that the lower numbered terminal was negative with respect to the one above it, and therefore that the recording wire nearer the tip was excited earlier than the one a millimeter behind it. The negative deflections on channels 3 to 7 demonstrate transmission of the impulse toward the center of the septum, as do the positive deflections on channels 8 to 10. These qualitative observations are supported by measurements of the peaks of the bipolar records which show exact time of local activation in milliseconds before or after the time reference.

The cavity potentials in the unipolar records reveal that the earliest sign of activity (in this case a negative deflection denoting movement of depolarization away from the recording point) in the left cavity (position 1 or 2) oc-
Fig. 3. Similar potentials from an electrode across the basal septum; excitation entirely from left. Details as in fig. 2. Discussion in text.

In the same experiment, an electrode across the basal septum showed activation entirely from the left (Fig. 3). Channels 1 to 5 and 11 through 14 in the unipolar records were in the left and right cavities respectively. Bipolar records show progression from left to right as indicated by the downward deflections on channels 6 to 9 and quantitated by exact measurements of the peaks of the bipolar records.

Normal septal activity in four experiments is plotted in fig. 4, 5 and 6. Fig. 4 is based on four parallel electrode positions in the mid upper septum. Time of local activity is noted at the proper position along each insertion. The earliest recorded muscle activity was along insertion "C" at the endocardial surface on the left side. From there, it proceeded along the endocardium and toward the center of the septum. Activity on the right side of the septum began 7.5 milliseconds later along insertion "D". This activity also proceeded endocardially, and from the right surface toward the center of the septum. The latest recorded activity (22 milliseconds) was near the midpoint of the basal insertion ("A"). The data have been analyzed by superimposing wave fronts (isochronous planes) at 5-millisecond intervals on the drawing of the tissue. These show invasions, initially from the left and...
later from the right, both proceeding toward the center.

Fig. 5 shows eight parallel insertions in the septum. Insertion 11 shows the earliest activity recorded in this experiment, at 4.5 msec. before the time reference, on the right endocardium. The earliest activity recorded on the left was 2.5 msec. later, at 2.0 msec. before the time reference, along the same insertion. There is rapid excitation of the apical endocardium on both sides at an apparent velocity which ranges from slightly larger values down to 1 m./sec. The endocardial velocity near the base of the heart is lower. Velocity through the muscle mass is less than 0.5 m./sec. All insertions except the upper anterior (number 18) show double envelopment. Cavity records indicated nearly simultaneous activity on both sides. A number of insertions in this experiment were not parallel to those shown here and have been left out to simplify the figure. Data from these insertions are in perfect accord with what has been indicated.

Fig. 6 gives data from an experiment in which, after registration of normal septal activity, a number of extrasystoles were elicited between adjacent points on the multipolar electrode; the insertions were the same for all recordings. The upper left diagram shows six spots where the electrode was inserted through the right ventricular wall. The other diagrams show times of activity along electrodes inserted into the septum at corresponding points. In the normal beat, earliest activity was on the left side (electrode insertion 1); the usual double invasion appeared along the three anterior electrodes, while the excitation was entirely from the left side along the three posterior insertions. In the beat labelled Ectopic 1, stimulation was on the left endocardial end of the upper anterior electrode. In the beat labelled Ectopic II, stimulation was at the right endocardium on the same electrode.
The Lead II electrocardiograms sketched below the diagrams show marked changes from the normal. The absence of potential change in the early portion of both ECG's is best explained by the postulate that activity spreads equally toward both body electrodes. In some extrasystoles, potentials were seen at the limb leads from the time of stimulation.

The first extrasystole spread with a rapid component along the left endocardial surface and a slower invasion from left to right through the muscle. Due to the transmission from the left, there was no sign of fast conduction along the right endocardium. In these records, the time required for septal activation during the extrasystole is 59.0 milliseconds compared to 22.5 milliseconds for the normal, an increase of 36.5 milliseconds.

The second extrasystole spread from its origin on the right side along the three anterior insertions and the lower left insertion. However, there was double envelopment along the mid-posterior insertion and a spread from the left on the upper-posterior insertion. This indicates that the fast conducting system on the left endocardium participated in transmission of the extrasystole. The time required for septal activation in Ectopic II was 45 msec. Typical velocities of endocardial excitation for the normal beat and the extrasystoles in this experiment are shown in table 1. In this experiment velocities were calculated for 25 electrode combinations in the normal beat and in five extrasystoles; in other experiments, velocities were calculated where possible. Since the drawing is somewhat simplified, exact calculation of
TABLE 1.—Endocardial velocities for several points in the normal beat and the ectopic beats in fig. 6. Velocities calculated in this fashion for normal beats or for ectopic beats which do not originate at one of the points involved are apparent velocities and merely set an upper limit to the actual velocity. The values between insertions 1 and 5 on the right are undoubtedly high for this reason.

<table>
<thead>
<tr>
<th>Electrodes</th>
<th>Distance (normal) mm.</th>
<th>Time (normal) msec.</th>
<th>Velocity Normal m/sec.</th>
<th>Time Ectopic msec.</th>
<th>Velocity Ectopic m/sec.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3 left</td>
<td>8</td>
<td>6</td>
<td>1.3</td>
<td>13</td>
<td>0.6</td>
</tr>
<tr>
<td>2-3</td>
<td>11</td>
<td>12.5</td>
<td>0.9</td>
<td>20</td>
<td>0.6</td>
</tr>
<tr>
<td>2-5</td>
<td>10</td>
<td>11.5</td>
<td>0.9</td>
<td>35</td>
<td>0.3</td>
</tr>
<tr>
<td>1-3 right</td>
<td>13</td>
<td>2.5</td>
<td>5.2</td>
<td>8</td>
<td>1.6</td>
</tr>
<tr>
<td>2-3</td>
<td>15</td>
<td>12.5</td>
<td>1.2</td>
<td>16</td>
<td>0.9</td>
</tr>
<tr>
<td>2-5</td>
<td>22</td>
<td>13.5</td>
<td>1.6</td>
<td>40</td>
<td>0.6</td>
</tr>
</tbody>
</table>

velocities through the muscle by construction of isochronous planes may be slightly inexact. However in both the normal beat and the extrasystoles, velocity through the muscle falls between 0.3 and 0.5 m./sec.

DISCUSSION

Discussion of the pathway of excitation may necessitate an idealized picture of the heart. Our results were obtained mostly on small dogs of all ages. Among this group there were many anatomical variations; particularly as regards the left septal surface. In a few hearts this surface was smooth and gently rounded, but in most, it was deeply trabeculated and encroached on by the papillary muscles. The right septal surface was usually smooth and more adapted to the calculation of velocities, but here, too, there were variations in anatomy. To these variations our techniques, refined though they may be, add variability arising from slight errors in measurement of electrode position, shrinkage of the heart, and random inaccuracies inherent in the procedure for timing the potentials.

For these reasons, it is not possible to make statements which apply to every heart about the site of earliest activity, the exact velocity along the endocardium or through the muscle, or the contribution of the septum to the electrocardiogram. We have carefully tabulated results for every experiment. From these, a general pattern of septal excitation has appeared for the dog, and has been confirmed with some variation in goats and monkeys. This pattern is in agreement with the vector analysis of Burchell and to a lesser extent with the findings of Sodi-Pallares and co-workers.

Site of Earliest Activity. It could probably be assumed that an electrode terminal touched the site of earliest activity in the heart if the earliest sign of activity in the cavity (and in the electrocardiogram which usually shows its earliest deflection slightly later) coincided with or followed depolarization at the spot. Such a point has been found only on one or two occasions in over 1000 insertions into dog hearts.* However, in many experiments the earliest recorded septal activity occurred within one to three milliseconds of the earliest sign of activity in cavity records. During the first few milliseconds of ventricular depolarization, cavity records most often indicate that the activity moved away from the left cavity (negative potentials) and towards the right cavity (positive potentials). Movement from left to right in the septum is therefore present in early depolarization. In some experiments the right and left cavities showed simultaneous receding activity. When account is taken of cavity records, earliest activity did not occur on the right in any experiment. Several experiments have been undertaken to find the earliest site of ventricular activity. These have not yet been conclusive but they indicate that activity in the left wall and in the left septum is nearly simultaneous.

The potentials indicate that the site of earliest septal activity on the left is half way between base and apex in the central septum near the earliest point of branching of the left bundle. From this point, activity spreads over the lower endocardium at a rate of about 1 m./sec. and through the thickness of the muscle at 0.3-0.5 m./sec. As in the wall, activity proceeds from the endocardial surfaces into the muscle.

The right side is usually excited later than the left by five milliseconds or less. The site of

* Reference is to potentials in muscle and not to portions of the conduction system from which we have on occasion recorded, and which show activity before cavity potentials appear.
earliest activity on the right appears to be near the base of the anterior papillary muscle. From this point the excitation advances as it does on the left, with an endocardial velocity in the lower septum of about 1 m./sec. Records from insertions into the posterior and upper septum indicate these parts of the septum are often excited from the left side.

On both sides of the septum activity spreads more slowly near the base of the heart. Here the endocardial velocity approaches that (0.3 m./sec.) for the thickness of the muscle, although the velocity is more often intermediate (near 0.6 m./sec.). This may indicate mixtures of tissues conducting at the rates of 1 m./sec. and 0.3 m./sec.

As in the wall, there was no indication that excitation in the septum is controlled by the individual muscle bundles that make up its mass, or by muscle fiber direction. Although the normal excitation passes from base to apex, as do the fibers of the septal endocardium, some components of excitation pass anteriorly, posteriorly and diagonally, crossing the superficial fibers at any angle up to 90°. Moreover, the extrasystoles indicated no preferential direction of activation, showing only the same velocities as those found in the two parts of the septum during the normal beat.

**Passage of the Excitatory Wave Through the Septum.** The movements of the activation waves are similar in the wall of the heart and in the interior of the septum except that, since the septum is excited from the endocardium on both sides, the majority of recordings show a double invasion. However, in the posterior and upper septum, there is a marked tendency for the septum to be excited from the left. Twelve per cent of our electrode insertions revealed excitation only from the left. Only one instance of excitation solely from the right was found. Where there is double invasion, there is a slight tendency for that from the left to be dominant. In evaluating such instances (60 insertions), we have found that 53 per cent of the invasions were dominantly from the left. The fact that one-eighth of the septum is excited entirely from left to right makes our total figure 60 per cent from the left.

In the wall there is evidence that the Purkinje fibers do not significantly penetrate beyond the endocardial surface except under the papillary muscles.† The same finding applies to the septum. Excitation does not penetrate any part of the thickness more rapidly and the velocity of passage approximates 0.3 m./sec.

**Contribution of Septal Excitation to the Electrocardiogram.** It is still too early for us to completely account for the peripheral electrocardiogram in the light of our findings. However, comparison of septal records in a number of experiments with records obtained in the free walls indicates that they are nearly simultaneous or that the septum is excited slightly earlier. The records in Fig. 2 and the plot of these in Fig. 6 are pertinent in this connection. Here the earliest septal activity (channel 3) was on the left side about three milliseconds after the earliest cavity potentials (channels 1 and 2) on that side, and about 10 msec. before the earliest negative potentials in the cavity on the right (channels 13 and 14). During the time when the electrode in the left cavity revealed receding activity (negative potentials), that in the right cavity showed approaching activity (positive potentials) until the right septal endocardium became active. This period was coincident with a downward deflection (positivity of the right forelimb with respect to the left hindlimb) in the electrocardiogram (channel 16) indicating a spread to the right and/or upward in the septum. The dog's septum lies in such a position that excitation from left to right alone would produce a downward deflection in Lead II.

Hecht‡ has reported potentials from the right cavity in humans which are similar to

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† The apparent velocity in the lower septum varies from 1 m./sec. to much higher values. In most cases all of the apparent velocities can be resolved into a number of components travelling at the stated velocity. As in the wall (6), true velocity can be determined only by connecting points simultaneously excited to determine consecutive positions of the wavefront.

‡ The finding by others that most of the wall thickness is simultaneously excited is probably due to the large electrodes and/or unipolar recording techniques employed. We have reexamined many records without finding this to be true.
ours in that there is an early positive deflection followed by a negative deflection. Correlation of septal activation with the ‘Q’ wave in Lead II has been possible in a number of our experiments where the records indicated earlier activity on the left of the septum. In four experiments in which the septal endocardium seemed to be excited simultaneously on both sides, this deflection was missing. While this correlation is not always possible, particularly when recording necessitates moving the heart in the chest, all of the facts are consistent with the hypothesis that septal activation gives such a vector during the first few milliseconds.

As has been stated, there may be simultaneous activity in the left wall and left septum in the first few milliseconds of ventricular activation. The earliest wall activity consists of a movement from endocardium to epicardium in the anterior (and possibly the posterior) wall which would give potentials predominantly in the antero-posterior plane and would therefore not affect the frontal plane vector derived from septal activity in the first few milliseconds.

It is not now apparent what contribution activation of the septum makes to the later portions of the QRS. Much of the septal activity is neutralized within the septum, and the direction of septal excitation during this period would be predominantly to the right and upward at a time when peripheral leads indicate that the heart is being excited predominantly to the left and downward. Moreover, septal activation is usually complete in 25 milliseconds, and on only one occasion did later septal excitation take place during the period when the ECG indicated a slowing of the above vector (after the peak of ‘R’ in lead II). A septal contribution to the later portion of the QRS seems very unlikely.

Factors Controlling Septal Excitation. We have examined the septal endocardium for Purkinje tissue using the bulk staining procedure of Lewis and have achieved results similar to his.

Although we cannot definitely state that the Purkinje tissue carries the rapid endocardial activation of the wall, and although we cannot prove that septal activation is similarly controlled, we believe that our physiological findings confirm the anatomical findings of Tawara, Lewis and Rothschild, and many others with respect to Purkinje tissue. Our picture of endocardial excitation in the septum is of a system conducting at about 1 m./sec., which will conduct at the same rate when excited artificially. This system extends through all of the septum except that, as Lewis has said of the Purkinje system, “the network does not appear to be well developed toward the tricuspid valve once the papillary muscle is passed” and on the left “the whole subendocardial space is richly lined except for a small area immediately beneath the aortic valves on each side of the main left division.” The regions immediately below the valves on both sides showed a slower endocardial velocity in our experiments.

The differences in apparent velocity between the septal and the mural endocardium during normal excitation may be ascribed to the fact that the septal endocardium is excited from a relatively punctate source, while the mural endocardium receives the excitatory wave from fibers travelling around the septum on both sides and from others traversing the cavities as false tendons. Extrasystoles in the wall show the same characteristics as those in the septum.

Septal conduction in extrasystoles allows prediction of spread in bundle branch block. The impulse originating at one point is transmitted by both muscle and Purkinje conduction at rates of 0.3 to 0.5 and 1.0 m./sec. respectively. It seems obvious that the increased time to excite the septum as in fig. 6 can account for almost all of the prolonged duration of QRS in bundle branch block. This increase in septal activation time is not the result of a block of any sort. Examination of the records in fig. 6 demonstrates that the extrasystolic impulse crosses the septum at about the same rate as the normal beat. The claims* that there is a “site of delay” and that the portions of the septum supplied by the left and right bundle are anatomically separated are unsupported by these studies.

The conduction velocity of 1 m./sec. which we have found for the lower septal endocardium is half of that determined for the false tendon.
in the dog by Draper and Weidmann. This difference may represent a true decrement in velocity in the distal portions of the conduction system. It may alternatively be due to a mixture of Purkinje and muscle velocities on the endocardial surface. In our previous ex-
periments, we could find no evidence to sup-
port any theory of rapid conduction by other
than Purkinje tissues. The findings in both the
wall and the septum can, we believe, be best
explained by the Purkinje system. Unsuccessful
attempts to demonstrate existence of this tis-
sue in the dog must therefore be considered
evidence for difficulty in anatomical delinea-
tion rather than proof that no such tissue
exists. Within the septal muscle there is evi-
dence that conduction proceeds syncytially
without special control of penetrating Purkinje
tissue and, as in the wall, without connective
tissue or other barriers. The percentage of the
thickness excited from right or left seems a
function of the endocardial Purkinje fibers
distribution and the preponderance of excita-
tion from the left due to earlier activation of
the left endocardium.

Goal and Monkey Hearts. For reasons which
are not clear, the potentials obtained from
these animals show slower depolarization and
more injury than those from the dog. Results
in these animals have therefore never been as
detailed as we would like. In the goat, the po-
tentials do not permit the affirmation of the
finding of double envelopment, but the apex
is excited earlier than the base. In the monkey,
both apex to base spread and double envelop-
ment have been found with the exception that
the proportion of the septum excited from the
left has been much higher (80 per cent).

Summary

The earliest activity recorded in the inter-
ventricular septum is usually on the left near
the first branching of the left conducting
bundle. Most of the septum is
excited by double envelopment from both
endocardial surfaces. There is a slight pre-
ponderance of spread from the left.

The fast conducting system conforms in its
distribution to the Purkinje tissue. On stimula-
tion, it conducts at a velocity of about 1 m./sec.
It does not extend into the center of the septum.
Conduction through the center of the septum
is syncytial in character. There are no con-
nective tissue or other barriers to conduction.

A septal contribution to the electrocardio-
gram is probably most evident early in ven-
tricular inversion when only the septum is
active. This activity seems to correlate very
well with the "Q" wave in Lead II. The septal
contribution to the later portions of the QRS
is probably minimal due to a) the opposite
direction of the two main septal vectors, b)
the overriding of septal activity by activity in
the wall, and c) the fact that the entire septum
is usually excited in 25 milliseconds.

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