Severing either right or left bundle branch in the canine heart produces prolongation of QRS and a deformity of that complex specific for the branch severed. Analogous deformities of QRS have been identified in human electrocardiograms. In both species, increment of QRS interval in association with bundle-branch block has been ascribed primarily to slow speed of transmission over muscular non-Purkinje pathways in the septal myocardium. Characteristic deformity of QRS has been ascribed to dominantly unidirectional excitation of ventricular septum from right to left or from left to right, and to delayed development of forces of excitation in the free wall of the blocked ventricle.

These concepts imply functional discontinuity of the right and left divisions of the specialized conducting tissues at their terminal ramifications in the canine and human hearts. Morphological confirmation of this conclusion has not been accomplished. Purkinje fibers in dog and man are not as readily distinguished from ordinary myocardial fibers as in certain of the ungulates. Hence, tracing the course of the Purkinje fibers even in the subendocardial layer has been difficult and determination of extent of their penetration into the depths of the septum and free walls, thus far impossible.

In contrast to the enforced ignorance of the terminal ramifications of the conduction system in canine and human hearts is a reasonably informed state concerning these structures in the hearts of cows and goats. Whalen (1928) is credited with first having presented evidence for a transseptal myocardial Purkinje network as observed in a series of calves hearts. Cardwell and Abrams (1931) confirmed this observation, noting that, "In the case of the beef heart, our observations show that transeptal intercommunications do exist in all our carefully injected specimens." Ter Borg (1941) concluded, "that a division into a right and left half is nowhere found, but that there is a continuity throughout the networks not only via the septum, but also along the parietal wall."

That penetration of Purkinje fibers into the epicardial layers in the goat has a functional consequence which can be identified electrocardiographically has been documented by Durrer and Van der Tweel. Epicardial complexes from the lateral wall of the left ventricle had a QS form. Bipolar complexes from multiple sites along a line perpendicular to endocardium and epicardium began and ended at nearly the same time. At some points, excitation appeared to spread dominantly in an epicardial to endocardial direction. Only in the outermost layers of the ventricular wall could a dominant endocardial to epicardial movement of excitation be recorded.

If the ventricular septum of the goat and calf is completely traversed by Purkinje fibers, will severing of a bundle branch be attended by changes in duration and form of QRS complex comparable to those occurring in canine and human hearts under similar circumstances? Hecht, in discussing the findings of Durrer and Van der Tweel recounted in the preceding paragraph, recalled unsuccessful efforts by Alfredson, Wilson, and himself to produce bundle-branch block in calves by the technique commonly applied in inducing canine bundle-branch block. Hecht concluded: "The inference, of course, is that because of the very well developed conduction system in cattle, and in ungulates in general, conduction was accomplished without difficulties from the contralateral side via the ramifications of an excessive Purkinje system."

Alfredson and Sykes (1940) did report some increase in the QRS interval on section
Standard limb and unipolar extremity leads from calf 1.

of the right bundle (average 0.013 second in eight calves) or in the left bundle (average 0.005 second in six calves). The form of complexes showed some change with induction of left bundle-branch block but very little with block of the right bundle.

In the course of studies on action potential in the atrioventricular conduction system in calves, right and left bundle-branch block were produced on multiple occasions. In the direct epicardial and cavity leads, the deformity of complexes was sufficiently characteristic to permit prompt recognition of the type of block. Inasmuch as the published electrocardiograms of Alfredson and Sykes included only the standard limb leads which leave in doubt certain points regarding the consequences of transecting a bovine bundle branch, electrocardiograms representative of our experience will be presented here.

Methods

The records presented were derived from newborn calves. Anesthesia was accomplished by intravenous administration of pentobarbital (Nembutal) sodium, 25 mg./Kg. of body weight. Artificial respiration was maintained once the thoracic cavity was entered. All electrocardiograms were recorded on the beating heart in situ.

Electrocardiograms in the experiment where right bundle-branch block was produced were recorded on a Sanborn Twinbeam direct writing instrument. Unipolar tracings were made by the Wilson central terminal method. Bipolar tracings were derived from a multiple terminal needle electrode supplied us through the kindness of Dr. D. Durrer.

The tracings from the experiment in which left bundle-branch block was produced were recorded on a Sanborn Twinbeam photographic instrument.

The right bundle branch was severed by placing a loop of thread around the moderator band in its course across the right ventricular cavity from septum to parietal wall. Thread and band were drawn through the needle wound, exposing the band which was then cut. The left bundle branch was transected with a thin-bladed scalpel introduced through the anteroseptal portion of the left ventricular wall.

Results

EXPERIMENT I:
RIGHT BUNDLE-BRANCH BLOCK

In figure 1 are reproduced standard limb and unipolar extremity leads recorded before thoracotomy. These records, made at a roller speed of 50 mm. per second and a sensitivity of 1 cm. = 1 mv., are characterized by small ventricular deflections in all leads. The QRS complex has a QS form in the three standard leads, whereas aVR is a monophasic R and aVL, a qR.

Figure 2 is composed of direct unipolar records made at N/10 sensitivity at a roller speed of 50 mm. per second (time lines, 0.02 second), as are all subsequent records in this experiment. On production of right bundle-branch block, the QRS interval increased 0.02 second. Noteworthy changes in form of QRS were: (a) the rS complex of the right anterior surface changed to an Rs, the upstroke of R being notched, and the intrinsic deflection occurring at least 0.02 second later than in records from the same site made before block; (b) the rS complex of the right cavity lead changed to an RS, the upstroke of R being notched; (c) leads from the left surface and cavity disclosed widening of terminal portion of complex without other change in form.

Figure 3 is composed of unipolar left cavity leads before and after right bundle-branch block serving as reference for bipolar leads made from endocardial, midwall, and epicardial levels with the multipolar needle electrode penetrating the anterior surface of the...
free wall of the right ventricle. Noteworthy in these records are: (a) occurrence of the rapid deflection in bipolar leads at essentially identical times in relation to reference lead, irrespective of epicardial-endocardial positioning of lead points in right ventricular free wall. Production of right bundle-branch block did not alter simultaneity of this fast deflection at the several points across the right free wall, but did result in, (b) delay in this rapid deflection of bipolar leads in relation to onset of QRS in reference lead by at least 0.02 second.

Figure 4 is composed of unipolar left cavity leads before and after right bundle-branch block, serving as reference for bipolar leads made from endocardial, midwall, and epicardial levels with the multipolar needle electrode penetrating the free wall of the left ventricle midway between base and apex, at junction of anterior and lateral segments of the wall. Noteworthy in these records are: (1) similarity of left free wall to right free wall as regards simultaneity of rapid deflection in bipolar leads whether from endocardial or epicardial sites; (2) occurrence of this rapid deflection in bipolar leads at the same time in relation to deflection of reference electrode, before production of right bundle-branch block as after production of the block.

EXPERIMENT II:
LEFT BUNDLE-BRANCH BLOCK

Figure 5 is composed of unipolar electrocardiograms made from points on the anterior surfaces of the right and left ventricles and
from intracavitary leads in each ventricle, both before and after production of left bundle-branch block. Noteworthy changes following production of block are these: (a) the QRS interval is increased by about 0.02 second following production of left bundle-branch block (time lines at 0.04 second); (b) the QS deflection of the left ventricular cavity lead prior to left bundle-branch block becomes an RS deflection after block and the RS deflection of the lead from the left surface becomes a monophasic R wave; (c) the form...
of complexes recorded from the right ventricular surface and cavity remains unchanged after left bundle-branch block except for widening of the terminal S deflection in both surface and cavity complexes.

Discussion

The 0.02-second prolongation of QRS interval following block of the right or the left bundle branch in these calves was relatively slight when the fact is recognized that the heart of a newborn calf is as large or larger than an average normal adult human heart. However, even this degree of prolongation of QRS implies a lengthening of the pathway of conduction by 4 cm. if the rate of spread is the same in the Purkinje network as in the main bundle branches of the bovine heart, i.e., 2 M. per second. Question remains, therefore, whether the transeptal communications between the right and left divisions of the conduction system are quite as free and open as the observations of anatomists suggest.

Moreover, the alterations in form of QRS which occur following block of either bundle in the calf are remarkably similar to those which develop after the same procedure in canine hearts. The comment applies both to epicardial and to ventricular cavity leads. The appearance of an initial broad R wave in the lead from the cavity of the ventricle to which the bundle branch is blocked suggests that a myocardial excitation front moves across the septum from the unblocked toward the blocked side. The simultaneity of the descending limb of this cavity R with the intrinsic deflection of the R wave from the right surface is consistent with the absence of an appreciable interval between excitation of adjacent endocardial and epicardial points in that free wall (see figs. 2 and 3).

Similarity between behavior of bovine and canine hearts regarding the consequences of bundle-branch block may, to be sure, imply functional discontinuity of the right and left divisions of the conduction system in the calf as well as the dog; on the contrary, functional continuity conceivably could exist and delayed and aberrant excitation depend on some other factor or factors inherent in the phenomenon of bundle-branch block. Discussion of such factors does not fall within the scope of the present article.

Summary

The electrocardiographic consequences of blocking the right or left bundle branch have been recorded in experiments on calves. Block of either bundle was attended by lengthening of QRS interval by approximately 0.02 second and by changes in form of QRS paralleling closely those occurring in canine hearts under comparable circumstances. Significance of this parallelism to concepts of morphology and function of ventricular conduction systems in bovine and canine hearts is considered. Data reported here render problematic the concept of functional continuity of right and left divisions of the specialized ventricular conduction tissue in the bovine heart.

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Electrocardiogram of Bundle-Branch Block in the Bovine Heart
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