Development of the human cardiac conducting system

A. C. G. WENINK

Anatomisch-Embryologisch Laboratorium,
Wassenaarseweg 62, Leiden, The Netherlands

INTRODUCTION

It is tempting to speculate about the origin of the cardiac conducting system from consideration of its adult morphology. Such an approach may well account for the frequently stated opinion that the atrioventricular system is a remnant of the embryonic atrioventricular canal musculature (Mall, 1912; Mönckeberg, 1924; Lieberman, 1970). However, the actual way in which the adult structure evolves from the embryonic primordium is not at all clear and there are marked discrepancies in the literature. In particular, there is disagreement regarding the stage of development at which the atrioventricular node can be recognized. In part, this is probably a matter of definition, since nodal histology in the embryo differs considerably from that in the neonate and adult.

What precisely does the embryonic conducting system look like? How far does it resemble the adult conducting system? One way of answering these questions is to investigate embryonic hearts with the intention of ascertaining if any specialized tissue can be distinguished at sites where conducting tissue would be expected to be present in the adult. An alternative approach is to search for parts of the myocardium which are histologically different from the rest, irrespective of their situation, and then to trace the evolution of these structures. There is considerable evidence to commend the second approach, since several investigators have reported 'conducting' tissues in sites not readily explained by presently accepted concepts of development. Thus, Shaner (1929) reported the transient presence of a node-like structure in the calf fetus in the ventral wall of the right atrium posterior to the aortic semilunar valves. In the human fetus, a ring of tissue with specialized characteristics has been identified in the right atrioventricular anulus (Keith & Flack, 1907; Anderson & Taylor, 1972; Anderson, Davies & Becker, 1974c). Moreover, additional conducting tissue has been described in the adult golden hamster (Gossrau, 1971) and the adult guinea-pig (Anderson, 1972). Consideration must also be given to the position of the atrioventricular node in some congenitally malformed hearts, this structure being anterolateral to the right atrioventricular orifice (Anderson, Arnold & Wilkinson, 1973; Anderson *et al.* 1974a, 1974b).

In the present investigation, therefore, search has been made for parts of the myocardium which were histologically distinct. The findings have enabled a scheme to be constructed which not only accounts for the development of the normal conducting system, but also provides a plausible explanation for the abnormal dispositions of conducting tissue in man and animals mentioned above.
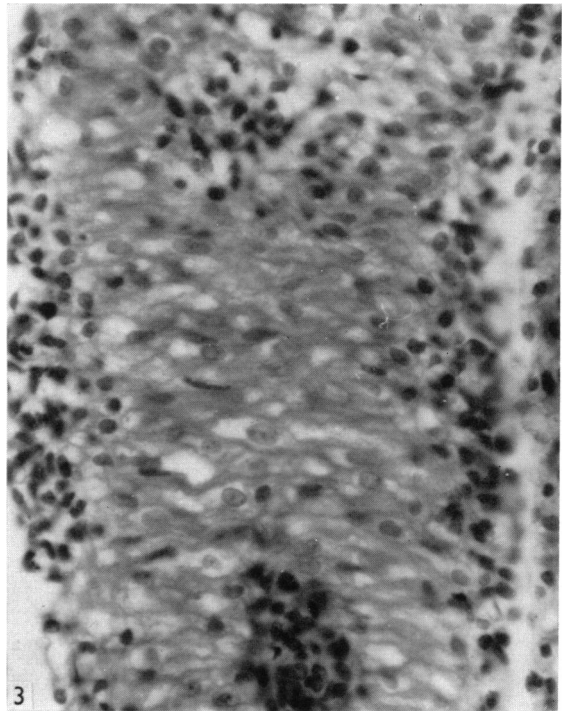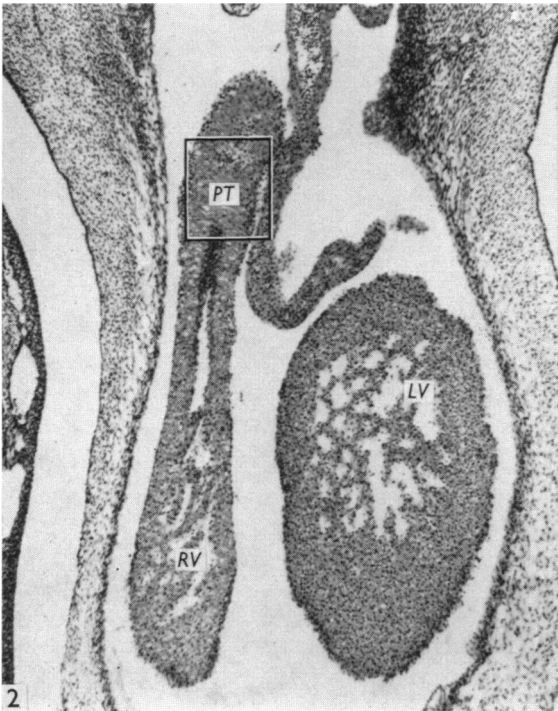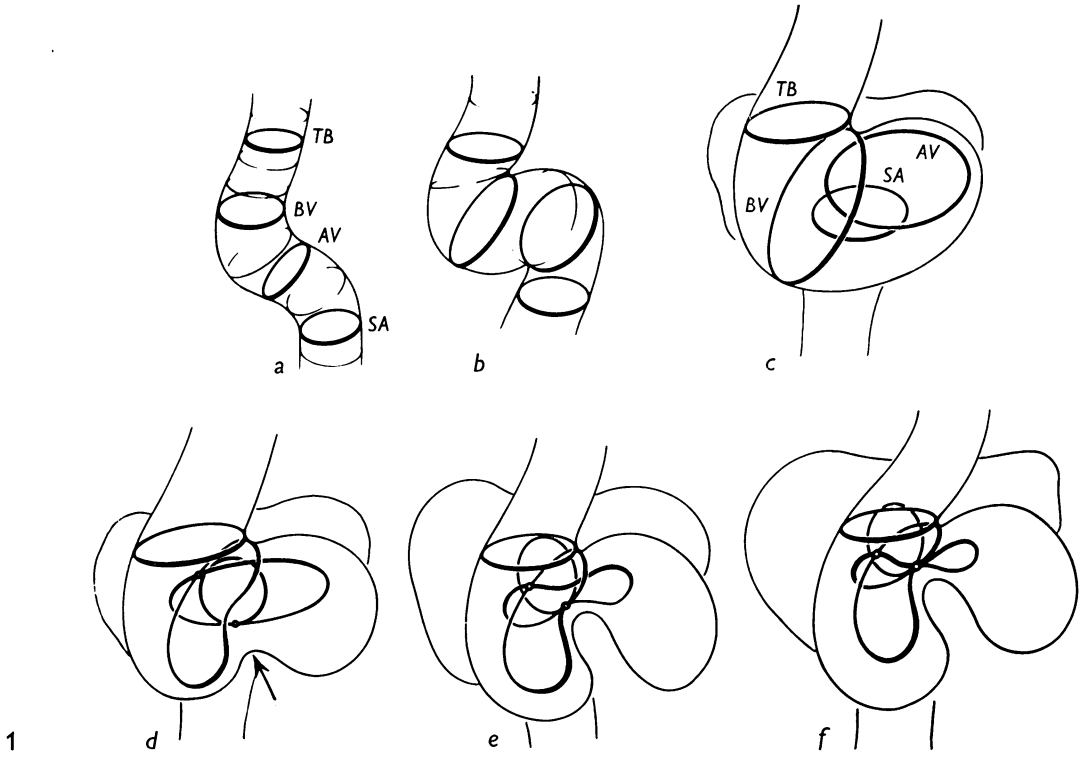
MATERIAL AND METHODS

The investigation was performed on eight human embryos and the heart of a 90 mm human fetus selected from the collection in Leiden University. The embryos varied in crown–rump length between 6·5 mm and 50 mm. All specimens were sectioned at 10 μm and stained with haematoxylin and eosin. The 90 mm specimen was stained by a modified trichrome method (Hoefsmit, 1967). All specimens were cut transversely, except for a 14 mm specimen which was cut sagittally.

In addition, by the kind permission of Dr R. H. Anderson, it was possible to examine a 15 mm embryo from the Manchester collection which had been cut transversely and stained with haematoxylin and eosin.

RESULTS

In the description of the material, attention will be paid to histological differences between different parts of the myocardium. The differences relate to the staining properties of the cytoplasm and the size and chromatin distribution of the nuclei. In general, cells which exhibit a bright red cytoplasm with haematoxylin and eosin; which possess relatively few myofibrils, giving the cell a 'smooth' homogeneous appearance (Walls, 1947; Licata, 1954); and which have relatively large nuclei with only slight chromatin staining, can be considered as representing part of the cardiac specialized tissue. The fact that such tissue is frequently isolated facilitates its recognition.

Attention will be paid also to the extensions of primitive connective tissue in the sulci of the heart which were described in earlier publications (Wenink, 1971, 1974).

In the youngest hearts the components of the primary heart tube were still recognizable. From distal to proximal it was possible to distinguish truncus, bulbus, ventricle, atrium and sinus venosus. Not only were there pronounced grooves between these components, but in addition endocardial thickenings were noted on their inner side and concentrations of loose mesenchymal tissue were seen externally. These features marked the transition zones between the basic component heart chambers.

However, yet another marker was present in these transitional areas. In these

Fig. 1. Diagram to illustrate the developmental changes of the interzonal specialized myocardial rings. (*A–C*): the looping of the cardiac tube produces a relative approximation of the rings in the bulbo-atrioventricular groove and in the posterior part of the atrioventricular groove. (*D*): the *AV*-ring shifts to the right and contacts the bulboventricular ring; arrow: the developing ventricular septum produces an invagination in the *BV*-ring in a posterior direction. (*E*): the *BV*-ring has joined the contact of *SA*-ring and *AV*-ring. (*F*): the anterior invagination of the *AV*-ring has joined these structures in the same area, thus dividing the *AV*-ring into right and left parts (see also Fig. 16).

AV, atrioventricular ring; *BV*, bulboventricular ring; *SA*, sinuatrial ring; *TB*, truncobulbar ring.

Fig. 2. Low power view of the heart of a 14 mm embryo. *LV*, left ventricle; *PT*, cranioventral wall of the pulmonary trunc; *RV*, outflow tract of right ventricle. × 39.

Fig. 3. Detail of Fig. 2. Note the clear cytoplasm and pale nuclei of the truncobulbar ring tissue. × 260.

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7A

7B
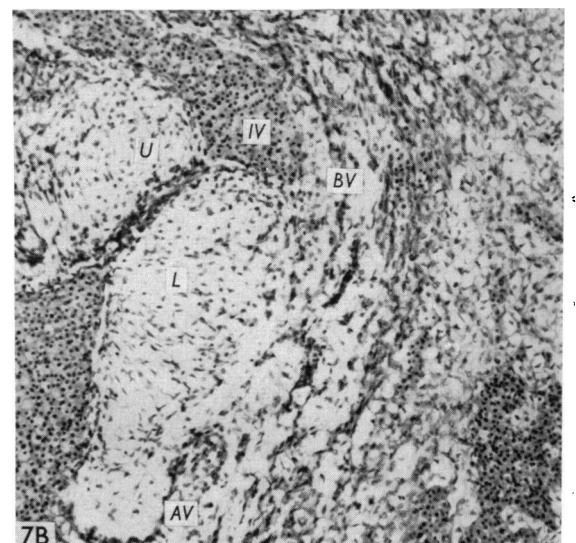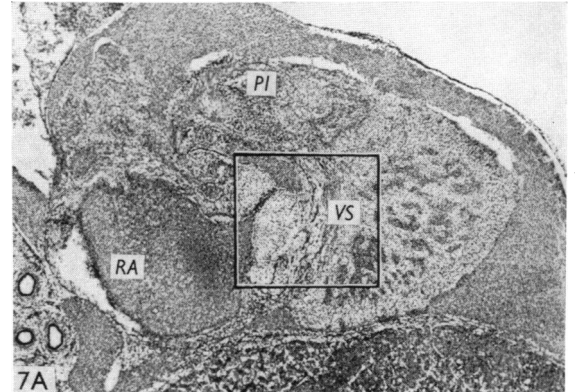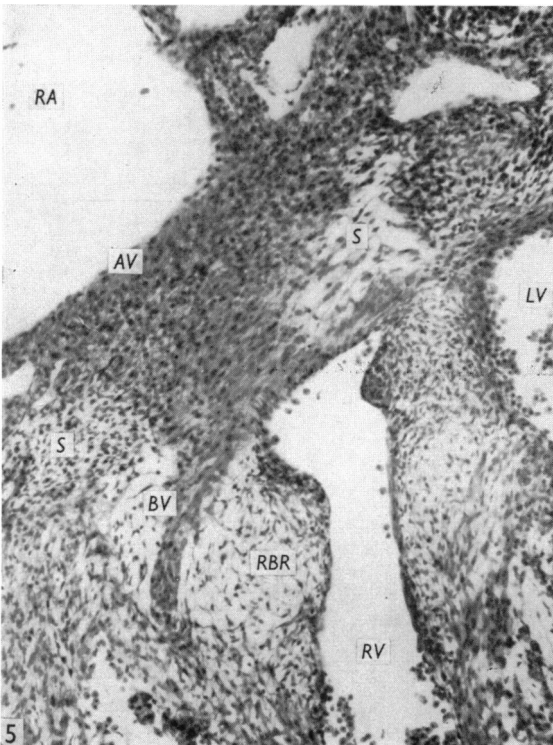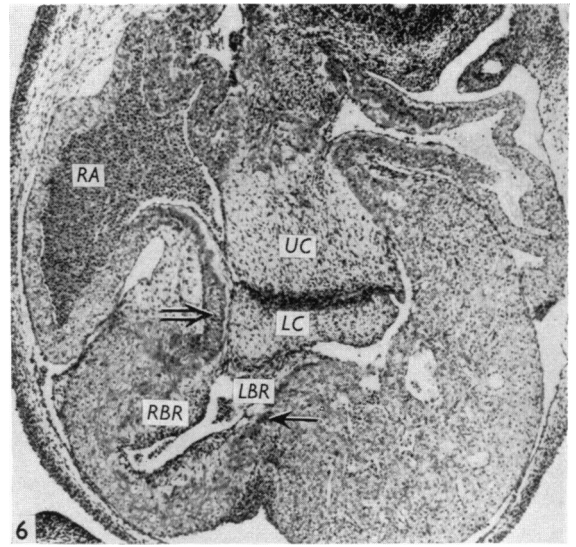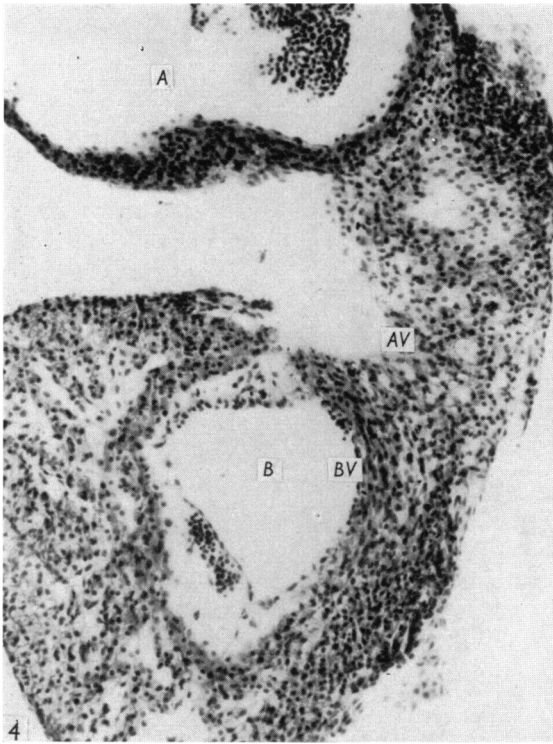
areas the myocardium exhibited the characteristics of primitive specialized tissue, as described above. Between the five parts of the heart, four myocardial rings were recognized in which the cytoplasm was strongly eosinophilic and looked homogeneous, while the nuclei were less dense than in the rest of the myocardium. These four rings will be termed 'trunco-bulbar', 'bulboventricular', 'atrioventricular' and 'sinuatrial' respectively. In Figure 1 the evolution of these rings during looping and canal migration is depicted. The septation processes in bulbus and truncus have been neglected in this scheme, but in the older stages it was necessary to distinguish between aortic and pulmonary rings, both of which have developed from the initial truncobulbar ring. Likewise, from the cranial part of the bulboventricular ring, a pulmonary component has been marked off. However, the pulmonary component seems to be of little significance for the development of the normal conducting system.

The various parts of the conducting rings were not equally clear at all stages. In the 6·5 and 7 mm embryos a truncobulbar ring at the level of the developing semilunar valves could not be established with certainty, but the very thin myocardium in this region was not directly comparable with that seen in other parts. From 9 mm to 50 mm, this tissue was easily recognized (Figs. 2 and 3) and the aortic ring was particularly well seen in the 50 mm embryo.

The bulboventricular ring was visible from the earliest stages. Its upper part was seen in the lesser curvature of the heart loop between bulbus and ventricle and between bulbus and atrium. Contact between bulboventricular and atrioventricular rings was clear in this sulcus in the 6·5 mm embryo (Fig. 4).

Here, and in the 7 mm specimen, this point of contact lay somewhat to the left of the bulbus. In the older embryos the point of contact had shifted to the right and took up a position dextrodorsal to the bulbus (Fig. 5), where it was close to the right bulbar ridge and the atrioventricular sulcus. In the 50 mm stage this contact had been broken by the development of intervening tissue from the atrioventricular sulcus. The contact between bulboventricular and truncobulbar rings lay somewhat more cranially. In older stages the pulmonary ring had split off and the bulboventricular ring then had a contact with the aortic ring. The left and ventral

Fig. 4. Transverse section of the heart of a 6·5 mm embryo. Note the contact between bulboventricular (*BV*) and atrioventricular canal musculature (*AV*). *A*, atrium; *B*, bulbus. × 105.

Fig. 5. High power view of the right anterior *AV*-sulcus area in the heart of a 17 mm embryo, to demonstrate the continuity of bulboventricular (*BV*) and atrioventricular (*AV*) musculature. *LV*, left ventricle; *RA*, right atrium; *RBR*, right bulbar ridge; *RV*, right ventricle; *S*, atrioventricular sulcus. × 105.

Fig. 6. Transverse section of the heart of a 7 mm embryo, to show the darkly staining bulboventricular (arrow) and atrioventricular (double arrow) specialized rings. *RBR*, right bulbar ridge; *LBR*, left bulbar ridge; *LC*, lower *AV*-cushion; *RA*, right atrium; *UC*, upper *AV*-cushion. × 39.

Fig. 7*A*. Sagittal section of the heart of a 14 mm embryo. *PI*, pulmonary infundibulum; *RA*, right atrium; *VS*, ventricular septum. × 22.

Fig. 7*B*. High power of Fig. 7*A*, to demonstrate the bulboventricular ring tissue (*BV*) passing ventral to the interventricular communication (*IV*). *AV*, atrioventricular ring musculature; *L*, lower *AV*-cushion; *U*, upper *AV*-cushion. × 105.
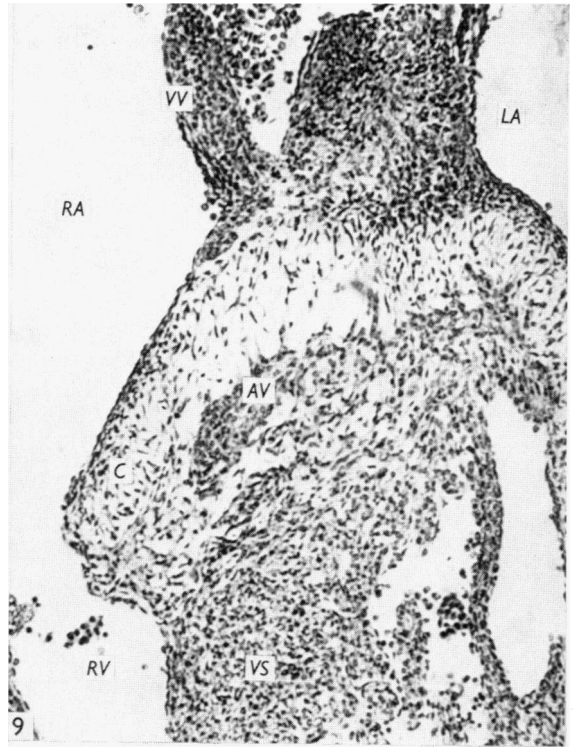
part of the bulboventricular ring had an intimate relationship with the left bulbar ridge, and passed apically to lie on the right side of the ventricular septum (Fig. 6). The lower part of the bulboventricular ring was established by the fusion of left and right parts towards the apex of the right ventricle. In young stages the bulboventricular ring could be followed throughout its full extent, but the connexion between ventricular septum and aortic base, which passed along the ventral and cranial boundaries of the interventricular communication in our 14 mm specimen (Fig. 7), was lost in older hearts.

As depicted in Figure 1, the left and ventral part of the bulboventricular ring changed its position during development. Growth of the muscular ventricular septum was considered to be the cause. Either the bulboventricular ring was taken up with the crest of this septum, or alternatively the caudal part of the ring was taken down by the outgrowing ventricular pouches. The ring gave off branches to the left side of the septum, as may be seen in the 15 mm specimen (Fig. 8).

Besides the contact with the ventral and cranial part of the atrioventricular ring, the bulboventricular ring also made contact with its dorsal and caudal part. This contact seemed to be facilitated by the septation process mentioned above. In the youngest specimens the contiguity was not well seen, but in older embryos a specialized bundle continued dorsocaudally astride the septum and ran without a visible transition into the atrioventricular ring. The latter, which passed down the septal crest beneath the atrioventricular cushions surrounded by loose connective tissue, was very compact (Fig. 9). Like the bulboventricular ring, this posterior part of the atrioventricular ring gave off branches to the left side of the ventricular septum (Fig. 10). The atrioventricular ring, visible throughout all stages, also changed its form and position. First, it was invaginated into the ventricular cavity, lying in the base of the lateral atrioventricular valve anlagen. Secondly, it too became involved in the septation process. While the dorsocaudal part proceeded ventrally beneath the atrioventricular cushions, the ventrocranial part ran dorsally above these cushions. The two were not in contact in the 14 mm specimen, but in older stages they joined each other dorsal to the atrioventricular cushions (now fused into one cushion) (Fig. 11). Between the anterior part of the atrioventricular

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Fig. 8. Transverse section of the heart of a 15 mm embryo, at the level of the roof of the interventricular communication (*IV*). Note the dark cells (arrow) streaming along the left side of the ventricular septum (*VS*). *BV*, bulboventricular ring musculature; *LA*, left atrium; *RBR*, right bulbar ridge; *RV*, right ventricle; *U*, upper *AV*-cushion. × 39.

Fig. 9. High power view of the heart of a 17·4 mm embryo, showing the posterior invaginated portion of the atrioventricular ring tissue (*AV*) on top of the ventricular septum (*VS*). *C*, right part of the fused *AV*-cushions; *LA*, left atrium; *RA*, right atrium; *RV*, right ventricle; *VV*, right venous valve. × 105.

Fig. 10. Transverse section of the heart of a 15 mm embryo. Note the cell bundles (arrow) coming from the posterior invagination of the atrioventricular ring (*AV*) and passing along the left side of the ventricular septum (*VS*). *L*, lower *AV*-cushion; *LA*, left atrium; *LV*, left ventricle; *PS*, primary septum; *VV*, right venous valve. × 39.

Fig. 11. High power view of *AV*-nodal area of a 17 mm embryo, to demonstrate the three components of the node: the musculature from the right venous valve (*VV*), the anterior invagination of the *AV*-ring (*AAV*) and its posterior invagination (*PAV*). *C*, cushion tissue; *S*, sulcus tissue; *VS*, ventricular septum. × 105.
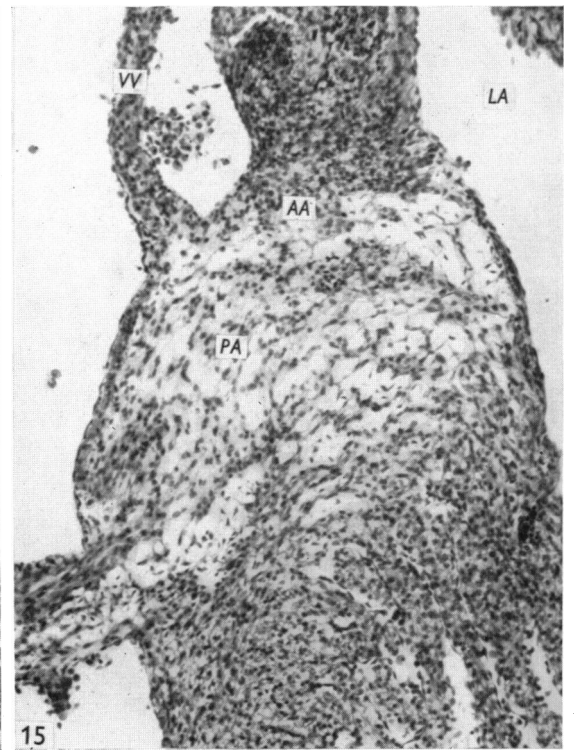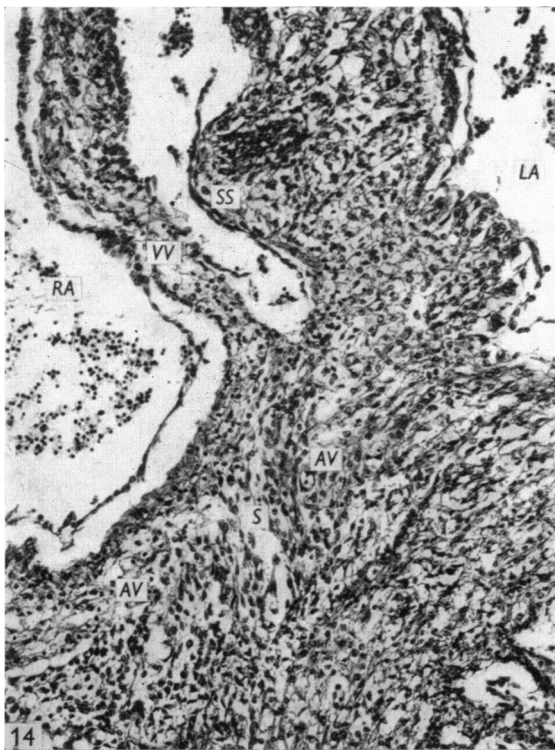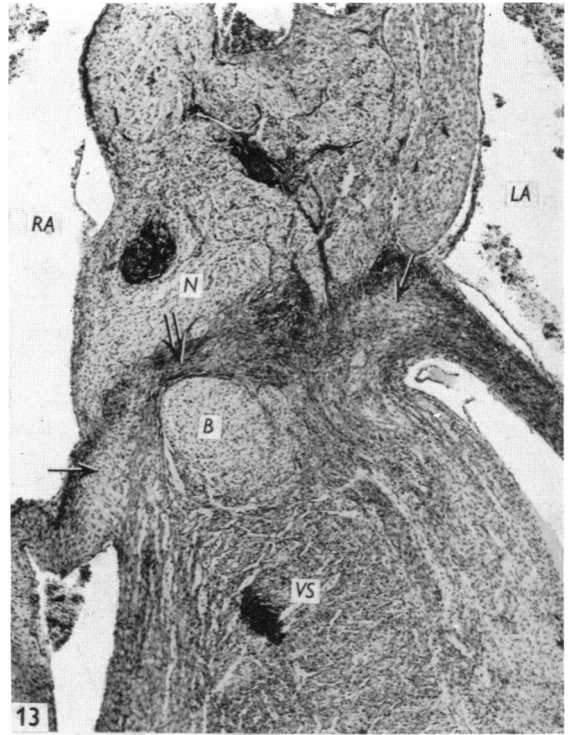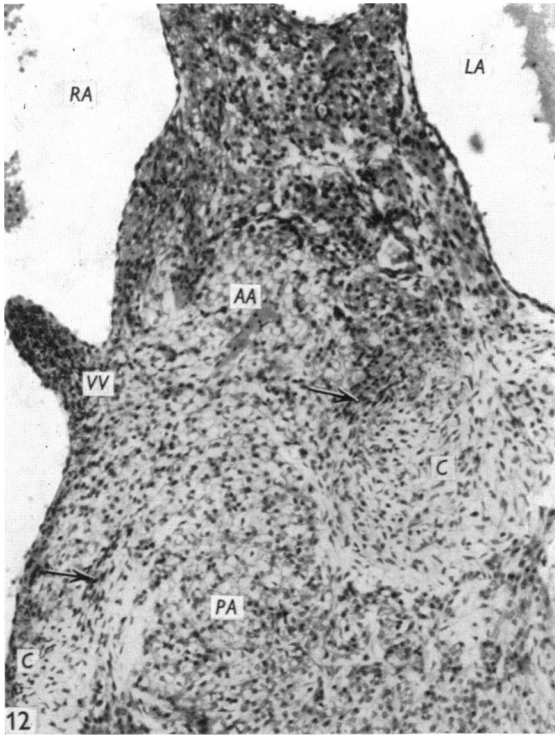
ring and the cushion, sulcus tissue was always present. In fact, this tissue could be followed from the aortic-atrial sulcus to the position mentioned. From here, it could be followed to the septum sinus venosi and the dorsal mesocardium on one hand, and to the caudal atrioventricular sulcus on the other. As was described in an earlier paper (Wenink, 1971), this tissue continuously surrounds the bundle on the crest of the ventricular septum. In our 50 mm embryo it appeared as a compact concentration of young fibroblasts (Fig. 12). It must be emphasized, therefore, that specialized tissue is always separated from the atrioventricular cushion by atrioventricular sulcus tissue, so that in sections dorsal to the atrioventricular cushion fibrous tissue can still be seen between the common bundle and the node (Fig. 13). From the above description it will be clear that the anterior part of the atrioventricular ring joins the posterior part on its upper aspect, the atrioventricular cushion intervening between the two like a wedge. Figure 14 shows a caudal section of the 29 mm embryo, in which the septation process has made a right and left atrioventricular ring out of the pre-existing common one.

The sinuatrial ring was invaginated into the atrial cavity at an early stage. The venous valves were bilaminate structures consisting of layers of both atrial and sinus musculature, the latter being the thicker component. Craniodorsally, this ring revealed a thickening from which extensions came down through both valves to make contact with the dorsal part of the atrioventricular ring. In older stages, where the left venous valve had become part of the atrial septum, the right valve seemed to be the most important as regards the contact with the atrioventricular ring. In a transverse section of our 17 mm specimen (Fig. 11) this contact with the sinuatrial ring was part of a triple contact between ring structures, the three elements being seen in the following ventrodorsal order: posterior part of atrioventricular ring, anterior part of this ring, and right venous valve. In a lower section of the same heart (Fig. 15) the anterior *AV*-ring component could not be distinguished, while the other two formed a single reticular structure.

DISCUSSION

It is clear that, in the developing heart, there is a very extensive specialized system with characteristics compatible with it being the precursor of the adult conducting system. Before this hypothesis can be validated, however, it will be necessary to

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Fig. 12. High power view of the heart of a 50 mm embryo, to show dark sulcus tissue (arrows) intervening between cushion tissue (*C*) and specialized tissue. *AA*, anterior invagination of *AV*-ring tissue; *LA*, left atrium; *PA*, posterior invagination of *AV*-ring tissue; *RA*, right atrium; *VV*, right venous valve musculature. × 105.

Fig. 13. Transverse section of the heart of a 90 mm fetus, to show the compact sulcus tissue (double arrow) dorsal to the atrioventricular cushion (arrows). *B*, proximal portion of the common bundle; *LA*, left atrium; *N*, atrioventricular node; *RA*, right atrium; *VS*, ventricular septum.

Fig. 14. High power view of a 29 mm embryo, to demonstrate sulcus tissue (*S*) intervening between the right and left posterior parts of the atrioventricular ring (*AV*). *LA*, left atrium; *RA*, right atrium; *SS*, sinus septum; *VV*, right venous valve. × 105.

Fig. 15. Transverse section of the *AV*-nodal area of a 17 mm embryo, to show the fusion of the nodal components. *AA*, anterior invagination of *AV*-ring; *LA*, left atrium; *PA*, posterior invagination of *AV*-ring; *VV*, right venous valve. × 105.

Posterior

Anterior

LAV

TB

SA

BV

RAV

16

AA

SA

PA

RBB

LBB
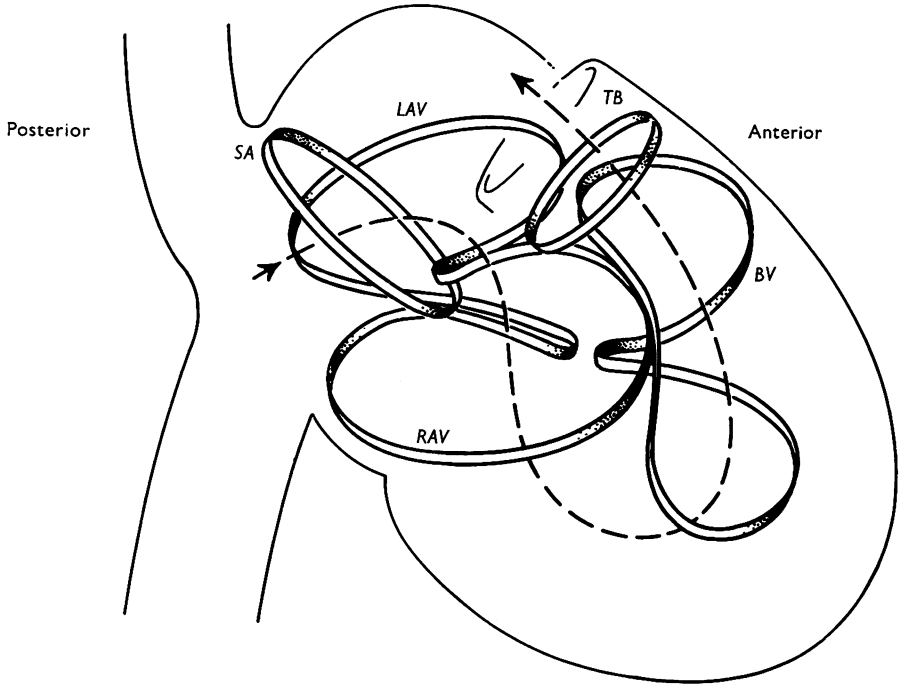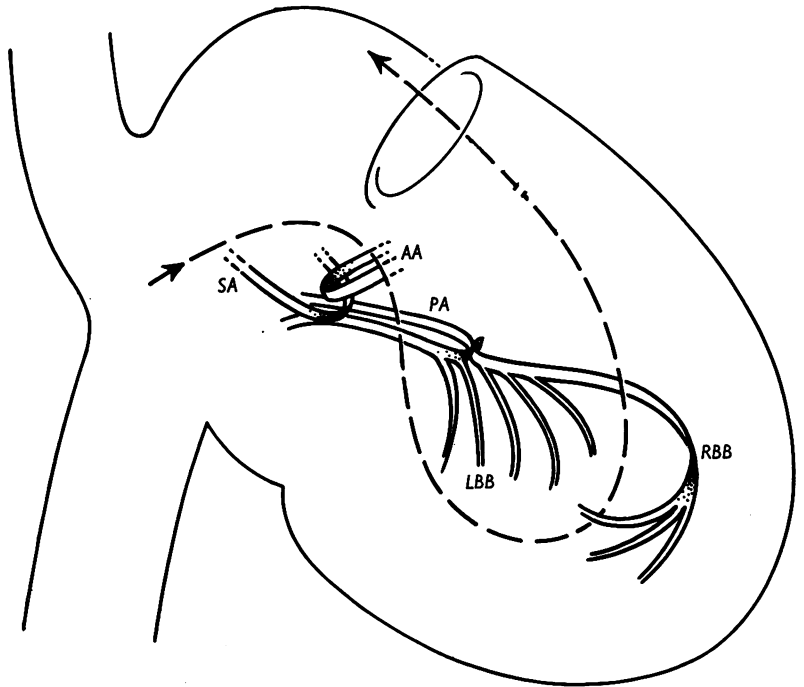
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establish the histological properties of this embryonic system using more advanced techniques, such as enzyme histochemistry and electron microscopy. However, leaving histological arguments aside, the localization of this presumptive conducting system in the embryo can explain many previously imperfectly understood features of the adult conducting system. It will be appreciated that the arguments presented are based on morphological considerations only, and that the problem of impulse conduction in the embryo is not within the scope of this work.

The concept of a series of myocardial rings being the phylogenetic precursors of the mammalian conducting system was propounded by Benninghoff (1923), who went so far as to ascribe a sphincter-like function to them. In general terms, this view was endorsed by German embryologists (Goerttler, 1963; Starck, 1965). However, explicit studies on these myocardial 'sphincters' have been largely restricted to the realm of comparative anatomy (see Heine, 1972). The distinction between the phylogenetic and the ontogenetic approach is, perhaps unintentionally, well demonstrated by Schiebler & Doerr (1963) in their dissertation on the development of the conducting system. Its first part is devoted to comparative anatomy and much attention is paid to specialized myocardial rings. In contrast, the second part, dealing with the histogenes and ontogeny, does not mention the rings and the authors are chiefly concerned with the times at which different parts of the well known atrioventricular conducting system first become visible.

Although the above discussion suggests that the phylogenetically established myocardial rings have not received much attention in the literature on human cardiac development, it must be stated that the atrioventricular ring has been the subject of several studies (Keith & Flack, 1907; Anderson & Taylor, 1972; Anderson *et al.* 1974*c*). However, the present study suggests that *all* the myocardial rings are essential structures in human cardiac development. Therefore, conclusions that the bundle of His is a remnant of the atrioventricular musculature (Mall, 1912; and many others), or that the bundle develops as an actively growing structure from the atrioventricular node (Walls, 1947) are no longer acceptable. Nonetheless, the impression must not be given that the entirety of all rings persists. It has already been emphasized that, during development, parts of this extensive system disappear. In particular, the connexion between the anterior part of the atrioventricular ring and the apical part of the bulboventricular ring is not represented in the adult conducting system. Neither is the connexion between the aortic ring and the top of the ventricular septum detectable in the adult heart. Consequently, only part of the bulboventricular ring is represented in the adult conducting system (Figs. 16 and 17). It can be hypothesized that the common bundle, and the right bundle branch as far as its extension into the trabecula

Fig. 16. Diagram to show the final disposition of the four specialized rings, as seen from the right side. The dotted arrow suggests the blood stream. Septation of the distal parts of the heart has been omitted, thus depicting only one truncobulbar and one bulboventricular ring. *BV*, bulboventricular ring; *LAV*, left part of atrioventricular ring; *RAV*, right part of atrioventricular ring; *SA*, sinuatrial ring; *TB*, truncobulbar ring.

Fig. 17. The same diagram as Fig. 16, omitting those parts of the ring system which do not contribute to the normal conducting system. *AA*, anterior invagination of the *AV*-ring; *LBB*, left bundle branch of dual origin; *RBB*, right bundle branch; *PA*, posterior invagination of the *AV*-ring; *SA*, sinuatrial ring.

septomarginalis, are remnants of the bulboventricular ring. However, the primitive conducting system does not so clearly involve the left ventricle. This explains why the left and right bundle branches are so different morphologically. It seems that the right bundle branch, being present before development of the ventricular septum, retains its primitive form. In the left ventricle, however, no such primitive structure is present. During development of the septum, cells of the bundle on its crest are probably taken down in an apical direction. This would explain the fan shape of the left bundle branch. This view is at variance with that espoused by Bersch (1973). Unlike that author, the present investigator was unable to define a left sided 'moderator band'. The evidence suggests that not only the bulboventricular ring but also the posterior part of the atrioventricular ring give off branches to the left side of the septum (Fig. 17). The left bundle branch, it would appear, has two different anlagen; and it is an interesting fact that its two fascicles have a different blood supply (Frink & James, 1973). The point of fusion of the bulboventricular and atrioventricular rings has not been determined with certainty. In previous presentations (Wenink, 1971, 1974) the transition from the left bulbar ridge, which envelops the right bundle branch and the distal part of the common bundle, to the atrioventricular sulcus tissue surrounding the proximal part of the bundle and the atrioventricular node, has been discussed. It is an attractive hypothesis that both connective and conducting tissues should meet at the same point, and it is suggested that this point lies relatively distally (Fig. 16) in the nodal-atrioventricular bundle axis. Regarding the atrioventricular ring, it is remarkable that, in late fetal stages, when its direct connexions with ventricular myocardium have disappeared, this ring is still present (Anderson & Taylor, 1972). Undoubtedly its central parts, brought together by the septation process, are the most important, and together with the sinuatrial ring these central parts are involved in the constitution of the atrioventricular node (Fig. 17). However, the right anterior part of the atrioventricular ring may also play an important role, particularly where it contacts the bulboventricular ring. In this position another contact can be made between two different rings, giving the possibility of forming a second node-like structure. It seems more than coincidence that this is the very position that Anderson et al. (1973, 1974a, 1974b) described for their 'anterior node' in malformed hearts. Of course it is obvious that in congenital cardiac anomalies the bulboventricular ring cannot have its normal localization; nevertheless some part of it could meet the atrioventricular ring to make the formation of the anterior node possible. Likewise, the connexion from this point to the top of the septum, that is the common bundle, could be formed by some part of the bulboventricular ring that is not normally incorporated into the definitive adult conducting system. To what extent the aortic part of the truncobulbar ring contributes to nodal connexions is not easy to say, but it is very near to the anterior infolded part of the atrioventricular ring. Perhaps, together with the cranial part of the bulboventricular ring, it does play a part in the establishment of those thick branches from the node to the base of the aortic mitral leaflet, which are sometimes observed in otherwise normal hearts (Gittenberger-de Groot & Wenink, unpublished observations).

The connexion between truncobulbar and atrioventricular rings can also account for the presence of a node-like structure in the ventral atrial wall just behind the

aortic semilunar valves, such as was described by Shaner (1929). He reported this 'interatrial node' in the heart of calf fetuses 13·5 to 90 mm in length. A similar explanation can be offered for the two additional atrial nodes of the golden hamster, which lie above the atrioventricular bundle and the aortic cartilage, as described by Gossrau (1971). Similarly, it is possible that the retro-aortic tissue of the guinea-pig (Anderson, 1972) is part of the truncobulbar ring.

The sinuatrial ring, which contributes to the atrioventricular node, provides in the embryonic heart a direct connexion between this node and the sinus node. In the adult heart the ring remnants, that is the venous valves, have become considerably attenuated, and many observers have been unable to identify specialized tracts between the nodes (Aschoff, 1910; Mönckeberg, 1910; Koch, 1913). It is indeed of great importance to define strict criteria for any tissue reported to be specialized (Janse & Anderson, 1974), but nevertheless, these criteria may vary with the developmental stage of the tissue. This statement is necessary, since observations on embronic material are not necessarily relevant to discussions concerning the existence of specialized atrial internodal pathways in the adult heart (Retzer, 1920; James, 1970; Janse & Anderson, 1974). Nevertheless, in the embryonic stages presently studied, it must be stated that the sinuatrial ring was distinguishable in the posterior atrial wall as a specialized structure connecting the primordia of the two definitive nodes. The impression is certainly gained that the sinuatrial ring must be the precursor of the sinuatrial ring bundle, described by Paes de Carvalho *et al.* (1959) in the rabbit atrium.

However, direct continuity with the atrioventricular node in the adult rabbit could not be established with certainty (Bojsen-Møller & Tranum-Jensen, 1972). In fact, this continuity might well have disappeared by becoming histologically 'unspecialized' like other parts of the ring system in the adult heart.

Finally, some attention must be directed to the sinuatrial node as being part of the ring of the same name. Chuaqui (1973) states that this node and the atrioventricular node appear to be homologous structures. However, the sinuatrial node must be different, since only one ring contributes to it.

In the light of the present study one is not surprised by the observations of Heintzberger (1974). She described a transient myocardial structure ventromedial to the left sinus horn in embryonic mice of 11 to 14 days, which looked exactly like the right sided sinuatrial node. Although the presence of such a left sided specialized structure at this stage is denied by Van Mierop & Gessner (1970), Heintzberger's photographs are very convincing.

To conclude, attention should be drawn to the terminology used in cardiac embryology. The concept of development of the conducting system arising from the present work provides for a clear distinction between the different parts of the primitive heart, such as Laane (1974) has requested. The conducting rings are interposed between sinus venosus, atrium, ventricle, bulbus and truncus. The truncobulbar ring is found at the level of the semilunar valve anlagen, whereas the bulboventricular ring defines the boundary between inflow and outflow parts of the future right ventricle. Indeed, the trabecula septomarginalis (moderator band) is a right ventricular junctional structure, and its anlage is already present *before* the ventricular septum makes its entry somewhat to the left of it. This view of the

conducting system can be considered as validifying the division of the heart tube proposed by Keith (1909).

SUMMARY

The development of the cardiac conducting system was studied in human embryos between 6·5 and 90 mm C–R length. It was concluded that, in the youngest stages, the interzonal areas between the different parts of the heart tube exhibit myocardial rings with morphologically specialized characteristics. These rings, already known from phylogenetic studies, are sinuatrial, atrioventricular, bulboventricular and bulbotruncal.

It is suggested that the conducting system develops as follows. Septation of the heart produces posterior and anterior invaginations in the atrioventricular ring. These invaginations, together with the sinuatrial ring, contribute to the definitive atrioventricular node. The sinuatrial node has its origin in the sinuatrial ring only.

Ventricular septation produces an invagination in the bulboventricular ring, which, by its fusion with atrioventricular ring musculature, produces the common bundle. The right bundle branch, at the boundary between bulbar and ventricular myocardium, similarly has its origin in bulboventricular ring tissue.

The left ventricle does not originally contain any specialized tissues. The left bundle branch only secondarily comes into existence by a fanning out of cells from both the atrioventricular and bulboventricular rings.

The 'four ring' theory explains certain examples of additional conducting tissue, as well as some congenital abnormalities, reported in the literature.

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