A Cineradiographic Study of the Snake Heart

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Cineradiographic studies on the cardiovascular system in snakes form the basis of this report. The method provides anatomical informations at the functional level and differs greatly from classical anatomical studies. The physiological interpretations involve timing of the various heart phases and the active role of the right atrium during ventricular filling. The snake ventricle has an incomplete septum and the admixture problem is discussed, as are some considerations regarding the pulmonary circulation and the reserve mechanism of the snake heart.

The comparative study of the circulation in vertebrates has been the object of renewed interest in recent years. The majority of papers available, however, discuss the amphibian (amphian) and mammalian heart and only scant attention has been paid to the circulation in other vertebrates. The reptiles represent the earliest group among vertebrates to become independent of a water environment as a requisite for life. Furthermore the snakes are the first amniotes entirely dependent upon lungs for their respiratory function. Such great evolutionary events are most probably related to the development of an efficient circulatory system. Among the reptiles the snakes represent an advanced group from an evolutionary point of view. In spite of this, the available reports on the physiology of the snake heart are few. More frequent are pure anatomical studies, including microscopic examination of fixed material and dissections on dead specimens. The present study deals with the snake heart. The elongated, cylindrical body form of these animals gives the investigator easy access to the circulatory system at any point he desires. The method employed was cinefluorographic angiocardiography of the living snake heart in situ. By this method direct information is gained regarding the functional anatomy and physiology of this heart, including the sequence of events and their timing.

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Methods

The material used for this study consisted of 6 specimens of the common grass-snake, Tropidonotus murinus and 4 vipers, Vipera berus. The animals weighed from 80 to 120 Gm. and ranged from 70 to 100 cm. in length. The approximate size of the heart was 2 x 1 x 1 cm. During the experiments the snakes were enclosed in polyvinyl tubes, perforated to allow for unrestricted respiration. After taking a survey film for orientation, a window was cut in the polyvinyl tube and the liver, lying 3 to 7 cm. behind the heart, was exposed. A thin polyethylene catheter (P.E. 70) was introduced in the post-caval vein which lies at the lateral aspect of the liver.

Repeated doses of 0.5 to 1 ml. 45 per cent Diopaque were injected at a speed of about 0.3 ml./sec. An under-couch tube with micro-focus (0.3 mm.) was situated 50 cm. below the table. An image intensifier 50 cm. above the animal, connected with a camera, completed the arrangement. In this way a 1:4 magnification was obtained before the image entered the intensifier, where the unsharpness factor is larger than for conventional roentgen films.

Results

The Sinus Venosus

The snake heart lies largely in the right half of the animal. The injection of contrast into the post-caval vein filled the sinus venosus which was seen well delineated. If the amount of contrast used exceeded 1 ml., a retrograde filling of the pre-caval vein occurred.

A small right, lateral indentation anterior to the middle of the sinus venosus formed a dividing point separating a small anterior

*During the operating procedure local injections of procane were applied.
and a larger and somewhat broader posterior part. The latter extended posteriorly to about the middle of the ventricle (fig. 1). Slightly posterior to the indentation arising from the left dorsal border of the sinus venosus, the left jugular vein was regularly seen in its course along the dorsal atrio-ventricular sulcus, running anteriorly along the bend at the left heart border. This interesting reminder of the earlier left anterior cardinal vein has its homologue in the coronary sinus and in the persistent left superior vena cava, (ligament of Marshall) in some mammals, including man (fig. 1, B, C, D).

Both the sinus venosus and the left jugular vein showed definite diameter changes, the former alternating and the latter synchronous with the contractions of the ventricle (fig. 2). The pulsations observed in the sinus venosus resulted from local muscular activity and seemed not to be passively transmitted from the filling and emptying of the adjacent ventricle (fig. 3, A, B). These pulsations must have been of significance in effectively moving blood into the right atrium.

The pulsations of the left jugular vein were of considerable interest. When the ventricle was dilated the vein was kinked at its left lateral bend. This kink, however, was straightened out during ventricular contraction as the vessel emptied its contents into the sinus venosus. These observed movements and diameter changes may aid the venous return, rather closely resembling the venous "leg pump" in man. This view is supported by the fact that the left jugular vein runs in the sulcus between the muscular walls of the atria and the ventricle.

The Right Atrium

The right atrium was filled with contrast medium through the sino-atrial aperture. This aperture is equipped with valves and is situated anteriorly quite close to the atrio-ventricular border. Initially the contrast medium filled the "cul de sac" of the atrial auricle which extended towards the anterior border of the sinus venosus. Later in the filling phase a bulging of the atrium toward the ventricle was observed. This bulging terminated in the right atrio-ventricular valves (fig. 1, B, C, D). These valves did not open until the atrial contraction had started, and consequently ventricular filling occurred only during atrial contraction. Duration of atrial contraction varied from 0.40 to 0.44 sec. (The timing refers to heart rates from 60 to 70 beats/min.)
The Common Ventricle

An essential feature of the reptilian heart (crocodiles excepted) is the incomplete intraventricular septum. Following the opening of the right intraventricular valves, the contrast medium sharply depicted the ridges in the right part of the ventricle (fig. 1, D). At the end of the atrial contraction the ventricle was completely filled with contrast medium in its right part, whereas the left part contained much less (fig. 4). A border between these incomplete right and left compartments could be seen. It originated slightly to the left of the atrio-ventricular valves and could be followed to a point at the left posterolateral aspect of the ventricle. This last point was marked by a small indentation, which was most clearly observed before the isometric contraction started (fig. 2, A, C).

The dilated ventricle was somewhat larger than half of the heart (fig. 2, A, C). The atrio-ventricular border was oblique to the longitudinal, transverse and sagittal axes of the animal and extended from anterior left and ventral to posterior right and dorsal. Consequently it was best seen in the left oblique position. The marked difference in density between the right and left parts of the ventricle gradually diminished during the first contractions after injection of contrast medium and was usually no longer discernible after 3 to 4 heart cycles (fig. 3). This was apparently due both to recirculation of the contrast medium through the lung and to right-left shunting.

The ventricular isometric contraction lasted from 0.13 to 0.17 sec. and the ejection phase from 0.28 to 0.34 sec. At the end of each contraction the left part of the ventricle seemed almost completely emptied while the right portion showed a varying residual volume ranging from about half of its size when full, to less than one fourth of this (fig. 5 A, B). The separation of blood between the right and left parts seemed better when the residual volume was small and when small amounts of contrast were used.

The Left Atrium

The left atrium in snakes is smaller than the right. The difference in size may have a bearing upon the fact that the pulmonary circulation is a rather new evolutionary development in reptiles. The left atrium was filled with contrast medium by the venous return from the lung and appeared indistinctly at the left antero-lateral portion of the heart, partly covered by the other chambers.

The Pulmonary Artery

Following ventricular contraction the pulmonary artery supplying the single right lung was the first central vessel discernible. This was true of both ascending and descend-
Figure 3
A: The ventricle in subcomplete contraction. The pulmonary artery is visible posterior to the heart. Both aortas show good definition, the left one also posteriorly. C: Later filling of the left part of the ventricle. Note the difference (A and B) in calibre between the sinus venosus and the post caval vein.

p.a.: pulmonary artery, a.o.: aortas, r.a.: right atrium, c.v.: common ventricle, p.c.v.: post caval vein, r.a.o.: right aorta, l.a.o.: left aorta.

In the latter phases the sinus venosus and the left part of the common ventricle were not filled. It originated slightly to the left of the right atrio-ventricular valves and to the right of the bordering line between the 2 parts of the common ventricle. It ran anterior and ventral to the 2 aortas and then posteriorly along the right dorso-lateral aspect of the heart. The pulmonary valves, when closed, could be seen bulging into the right portion of the ventricle at the end of the ventricular filling phase. During this condition the part of the pulmonary artery adjacent to the ventricle was shortened and correspondingly broadened (fig. 2, B, C). The diameter of the pulmonary artery was obviously smaller in the descending part. The variation in breadth at the base of the pulmonary artery might indicate a larger distensibility of this vessel compared to the other central arteries.

Right and Left Aorta

The 2 aortas were filled later than the pulmonary artery. The difference was most conspicuous when small amounts of contrast was used. The aortas were only faintly seen after the first ventricular contraction and best at the bend of the arches where some over-projection of the ascending and descending part took place. The right aorta originated more to the left of the 2 and the contrast density was most often somewhat less than in the left one. The right aorta in reptiles gives rise to the common carotid and vertebral arteries. The left aorta is unbranched. After a second ventricular contraction the left aorta, and to some extent the branches from the right aorta, showed better contrast filling (figs. 3, B, C and 4). The third contraction showed the right descending aorta to its junction with the left aorta a few centimeters behind the heart. The posterior part of the right aorta was considerably thinner than the left (fig. 6). The diameter of the 2 ascending aortas seemed approximately equal to the diameter of the pulmonary artery, except for the first ascending broad part of the latter.

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Discussion

The mode of venous inflow to the heart is clearly demonstrated by this new approach to the study of circulation in snakes. The apparent role of the sinus venosus and the left jugular vein in aiding the venous return seems of considerable interest to comparative cardiovascular physiology.

The timing of the various phases in the heart cycle of the snake, as revealed from the cinefluorographic films, is in good accord with the values obtained by Johansen from pressure measurements in the heart and great vessels of snakes. Likewise the numbers given for the duration of ventricular isometric contraction agree with those reported by Shannon and Wiggers for the frog and turtle heart.

The fact that ventricular filling occurs only during atrial contraction distinguishes the snake heart from the mammalian. Furthermore, the long duration of the ventricular activity as compared to the resting phase is remarkable.

There has been relatively little exact information regarding the central admixture of arterial and venous blood in reptiles (crocodiles excepted). According to older reports the reptilian heart presents a picture of a relatively inefficient organ which allows extensive mixing of arterial and venous blood. More recent studies, however, have shown that although some mixing takes place early in systole, this is chiefly left-to-right shunting and before the end of systole the turtle heart is essentially a four chambered one. Dynamic studies of the snake heart likewise point toward left-to-right shunting. The present study provides visual inspection of the ventricle and should be well fitted for an approach to the admixture problem. The left-to-right shunting, however, is not well demonstrated because only larger amounts of added blood will change the contrast density in the right part of the ventricle. A rather small right-to-left shunt was observed. This shunting resulted obviously in more venous admixture to the left aorta than to the right, which supplies the brain. The admixture was most pronounced when larger amounts of contrast were used. This resulted probably in an unusual expansion of the ventricle facilitating shunting. The films furthermore disclosed another interesting feature. This has to do with the earlier appearance of contrast in the pulmonary artery than in the two aortas. As a result venous blood, which undoubtedly occupies most of the right portion of the ventricle, initially flows into the pulmonary artery. This in turn may bring about a directional flow within the ventricle, more in favor of a left-to-right shunting, or no shunting at all, than of a right-to-left shunting.
Figure 6 shows the vertebral and carotid artery anterior to the heart. Posteriorly is seen the junction of the left and the much thinner right aorta.

p.a.: pulmonary artery, v.a.: vertebral artery, c.ca.: common carotid artery, l.ao.: left aorta, r.ao.: right aorta.

The great distensibility of the pulmonary artery, with the consequent enlargement at its base during filling, may lead to a significant pooling of blood and likewise act as a pressure adjuster. Pooling of blood in the pulmonary artery is also emphasized by Woodbury and Robertson. They further noted a muscular ring encircling the orifice of the pulmonary artery in turtles. They felt that this structure contributed to the dispatch of blood into the proper vessels. The present study on snakes does not confirm the finding of a muscular ring of functional significance at the orifice of the pulmonary artery.

Another point of considerable interest has to do with the amount of residual volume in the ventricle after a contraction. Shannon and Wiggers stated in their work that, unlike the mammalian heart, that of the frog or turtle retains a substantial residual volume of blood at the end of each ejection. The amount of residual blood was sufficient to cause a significant ejection in an induced premature contraction beginning during the isometric relaxation phase. The authors suggested further that the presence of such residual blood provides a mechanism by which these animals can increase their cardiac output. Such a reserve mechanism is unknown to mammalian hearts. Woodbury and Robertson failed, on the other hand, to support the statement that the turtle ventricle retains a significant volume of blood at the end of systole. The present study displayed variable conditions regarding the degree of ventricular emptying. The shifts observed in the amount of residual volume could not with any degree of assurance be attributed to a demand for an increased cardiac output. The present observations, however, give some support to the suggestion from Shannon and Wiggers. It may be mentioned particularly that the storage of blood in the snake heart is mostly localized to the venous side.

**Summary**

The present study has been possible by introducing modern roentgen technic into the study of the functional anatomy and physiology of the snake heart. The mode of venous inflow to the snake heart has been demonstrated. The timing of the various heart phases was easily read from films made at a frame speed of 32/sec. The short resting period of the snake heart and the more active role of the right atrium as compared to the mammalian heart are noteworthy. The problem of arterial and venous admixture within the ventricle is discussed, and essential features demonstrated. The amount of residual volume in the ventricle after a contraction varied. It could be observed most distinctly in the right portion of the ventricle. A possible cardiac reserve mechanism based upon this phenomenon is suggested.

**Summario in Interlingua**

Le presente studio esseva possibile gratias al introducendo moderne techniens de radiologia in le investigation del anatomia e physiologia functional del corde del serpente. Le modo del influxo venose del corde del serpente esseva demonstrate. Le inter-relation temporal del varie pliases del corde esseva facilemente constatate in cineradiogrammas fasi e a velocite de 32 imagines per secunda. Le breve periodo de reposo del corde del serpente es digne de attention. Le problema del intermixtion arterio-venose intra le ventriculo es discutite, e aspectos essential de illo es demonstrate. Le quantitate del volumino residue in
le ventriculo post le contraction es variabile. Ille po-
terv esser observate le plus distinctemente in le por-
tion dextere del ventriculo. Es suggeste le possi-
bilitate de un mecliauismo de reservas super le base de
iste phenomeno.

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