THE DEPENDENCE OF HEAD CURVATURE ON THE DEVELOPMENT OF THE HEART IN THE CHICK EMBRYO

By C. H. WADDINGTON

From the Strangeways Research Laboratory and Sub-Department of Experimental Zoology, Cambridge

(*Received* 10 *November* 1936)

(With Three Text-figures)

At about the end of the second day of incubation, the anterior end of the embryonic axis of an embryo chick becomes twisted and bent. The twist, which is a simple rotation around the main embryonic axis, brings the left side of the head in contact with the yolk and raises the right side to point vertically upwards. The bending throws the embryonic axis into a rather complicated shape, the essential feature of which is that the anterior tip of the head remains comparatively near to a point just posterior to the ears, while the whole region of neural tube and brain which lies in between these two points is bent into an arc. The posterior part of the arc curves out slightly to the left of the main line of the embryonic axis but much the greater part lies to the right of this line. In the concavity of the curve, on the right side, lies the heart.

In embryos cultivated *in vitro* it is not uncommon for these bendings and twistings to be reversed, so that the right side of the head lies underneath and the concavity of the arc of the head opens on the left side. In such embryos, whose peculiarities are presumably due to some unanalysed mechanical effects of the comparatively hard plasma clot, it is interesting to note that the heart always lies in the concave side of the head. That is to say, when the head curvature is reversed, so is the side on which the heart lies. This might be due to a parallel action of the unanalysed factors which cause the reversal of the head curvature, but it might also indicate a real causal connexion between the head curvature and the position of the heart, though it does not give any information as to which of these two is the cause and which is the effect.

Experiments in which the embryo has been cultivated *in vitro* after removal of the heart have shown that there really is a causal connexion between the development of the heart and the curvature of the head, and that it is the heart which affects the head curvature and not vice versa. The embryos were operated on in stages with between seven and twelve somites, the amnio-cardiac space being opened by a cut through the splanchnopleure, and the heart, which is still a fairly straight tube at this stage, dissected out. Small portions of the sinus region were usually left after the operation and could be seen pulsating on each side of the embryonic axis in the cultivated embryos, but they were not large enough to obscure the main effects of the operation and may be neglected.

The embryos were cultivated to stages with about twenty-five to thirty somites, when controls showed clearly the bending and twisting of the head. The operated embryos showed no sign of any twist, but lay flat with their original ventral surface still against the clot. The greater part of the bending of the head was also abolished, so that the embryonic axis was perfectly straight (Fig. 1). One component of the

Fig. 1.

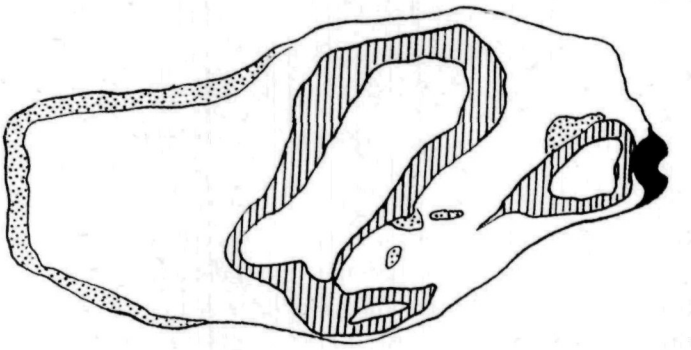

Fig. 2.

Fig. 1. No. 35–0104. The heart was removed from an embryo aged 44 hours, with eleven somites. The figure shows the anterior part of the embryo fixed after 23 hours' cultivation, when it had about twenty-five somites. Note the straightness of the axis, the large spaces in the head, and the small patch of beating heart tissue remaining on the right side.

Fig. 2. Same specimen, section through right eye. Mesoderm indicated by dots.

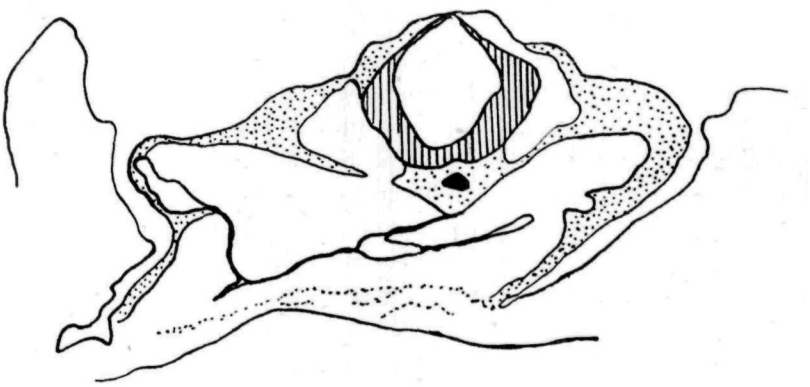

Fig. 3. Same specimen, section just anterior to ears. The foregut is compressed so that the lumen has almost disappeared except in the centre and on the left side. Mesoderm indicated by dots.

bending, however, occurs in these embryos quite dissociated from all the other components, which, as has been said, have been abolished by the operation. This component (the so-called cranial flexure) is the bending of the forebrain relative to the midbrain, which, in these embryos with a straight embryonic axis, causes the anterior tip of the head to curve sharply downwards into the underlying clot. The degree to which this curvature is developed is somewhat different in different embryos but it appears to be always present to some extent and one must conclude that it is produced by a process independent of the development of the heart.

The operated embryos illustrate one or two other points of interest. The aortic arches develop in a fairly typical way although deprived of contact with the remainder of the heart, which has been removed. The other main embryonic blood vessels are also formed, but, in the absence of circulating blood become enormously enlarged (cf. Hughes, 1934). This is particularly noticeable in the head, which is often almost completely hollow, the large empty cavities of the vessels being lined only with a little loose mesenchyme (Figs. 2 and 3). The notochord may sink away from the neural tube and become surrounded by a thin layer of mesenchyme. The foregut, if it is complete, may be very widely stretched from side to side across the enlarged head, its dorsal and ventral walls becoming very thin and enclosing only a narrow slit-like lumen; the lateral evaginations, however, usually develop their characteristic thick walls. In many specimens the foregut has been injured in the operation, the injury usually taking the form of a slit along the midline of the ventral wall, from which the heart has been loosened by sectioning the dorsal mesocardium. If the foregut has been slit in this way it may open out, the cut edges of its ventral wall joining up with the ectoderm of the lower side of the head so that the whole of the lower surface of the head becomes lined with foregut endoderm instead of ectoderm, which now forms only the upper and lateral surfaces. This entails a considerable increase in the total surface area of the head and thus aids the enlargement of the head caused by the swelling of the blood spaces. Even in these embryos one can often find the lateral evaginations of the gut; they form small pockets of thickened epithelium projecting inwards into the head. They do not reach the tissues which would normally develop with them into the visceral arches; but the presumptive arch mesenchyme seems to be independently differentiating, and can be seen as local patches of highly condensed mesenchyme lying amid the more loose tissue lining the ectoderm. It is impossible to state how far either the foregut evaginations or the arch mesenchyme could continue their differentiation when isolated from each other in this way.

SUMMARY

1. The heart was removed from chick embryos of seven to twelve somites, and the embryos cultivated *in vitro*. The operation abolished the normal twisting of the anterior part of the embryo on to its left side and the general bending of the brain region into an arc. These two processes therefore seem to be dependent on the normal development of the heart.

2. The embryos showed a bending of the forebrain relative to the midbrain, which is therefore independent of the development of the heart.

3. The embryonic blood system, including the aortic arches, developed normally in many cases, but the blood vessels became enormously dilated.

4. The lateral evaginations of the foregut and the visceral arch mesenchyme underwent the first stages of differentiation in atypical positions, seemingly independently of each other or of any other structures.

REFERENCE

HUGHES, A. F. W. (1934). *Philos. Trans.* B, **224**, 75.