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Organ-Forming Areas in the Early Chick Blastoderm.

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In attempting to locate the various organ-forming areas of the early blastoderm, a series of transverse and longitudinal cuts has been made at certain measured distances from the primitive pit in such a manner as to divide a single blastoderm of the head-process stage of development into a definite number (either 11 or 18) of median and lateral pieces. The developmental potency of each piece was tested in the chorio-allantoic membrane. Each part of the blastodisc is found thereby to have a certain capacity for development or specific organization, which becomes expressed in the form of specific tissues. Nearly 400 grafts have been examined histologically, a generalized analysis of which follows.

1. *Differences in developmental capacity along the antero-posterior axis.*[1] The portion of the area pellucida anterior to the head-process and that part of the area containing the posterior half of the primitive streak yield grafts much less frequently and invariably smaller ones than do those portions including either the node or the head-process. Also, the grafts from these portions exhibit a similar difference in the quantity of organ tissues produced, the node and process portions showing by far the greater variety and amount of tissues. Very striking is the demonstration that particular structures develop only from rather definite regions or areas of the blastoderm. So characteristic are some organ tissues of particular regions that we can speak of eye-forming, thyroid-forming, ear-forming, or mesonephros-forming levels or areas. The eye and thyroid-forming areas are associated with the anterior end of the head-process, ear farther posteriorly at the node level, while the center of the mesonephric area lies just posterior to the primitive pit (Fig. 1).

2. *Differences in developmental capacity along the medio-lateral axis.* Medio-lateral differences in the ability of the transplant to survive and grow as a graft are very noticeable. Graft frequencies are consistently higher for the median pieces, distinctly lower for the left, and lowest for the right pieces. Mesonephros develops, for example, with a frequency of 70% from median pieces, 18% and 11% from left and right pieces respectively. Also at the brain-

[1] Rawles and Willier, *Anat. Rec.*, 1934, **58**, (Sup.), 34.

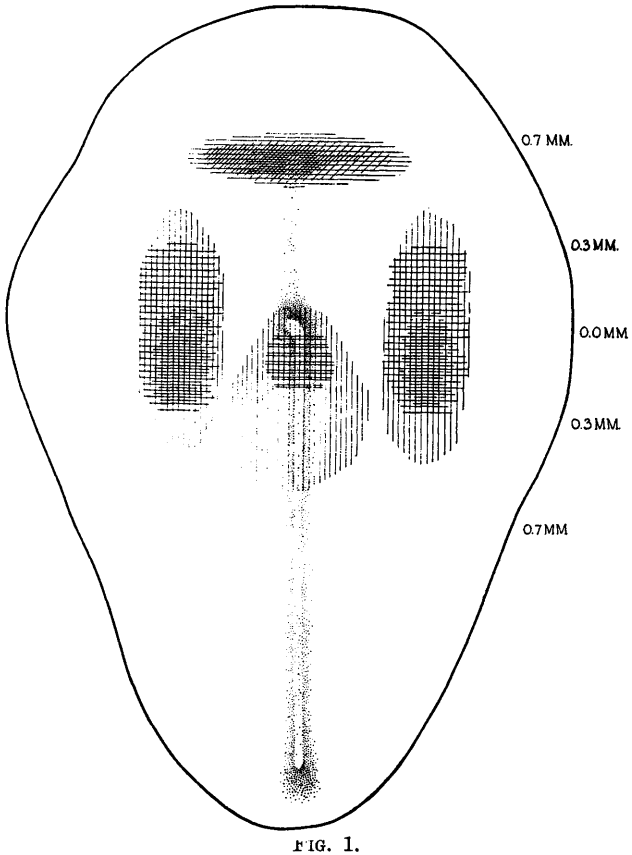

FIG. 1.

Map showing the position and shape of the eye-, heart-, and mesonephros-forming areas of a blastoderm of the head-process stage. The density of shading within areas indicates roughly the intensity of developmental potency. Only the region of greatest intensity of mesonephros formation, localized just behind the pit, has the power to form adrenal and gonad. X ca. 37.

forming levels nervous tissue illustrates very nicely the same kind of frequency differences, occurring in 100% of the median grafts, 70% of left and 50% of right. Further, differences in the size of grafts and the amount of recognizable differentiated tissue obtained from median and lateral pieces closely parallels the frequency differences.

Distinct medio-lateral gradations are evident as regards degree of differentiation attained by various structures. The eye, for example, which differentiates from a median piece may show all the constituent parts—retina, pigmented layer, lens—while grafts from lateral pieces seldom show more than the pigmented layer. In grafts from right pieces, particularly, a mere trace of the pigmented layer

is the sole representative of this organ. Similar conditions obtain with respect to differentiation of mesonephros where, again, in median grafts all the component elements are present and exhibit a higher grade of differentiation. Closely associated with the well-differentiated mesonephros of the median pieces, but absent in either of the laterals, are suprarenal and gonad (Fig. 1).

Many organs develop in obvious relation to medio-lateral organization: some from both median and lateral pieces, others only from median pieces, and still others only from lateral pieces. Structures occurring in both lateral and median grafts are brain parts, eye, ear, thyroid, mesonephros, skin, and the somite derivatives, cartilage, bone and muscle. Most of these structures developing in all 3 sections of a transverse level occur, as noted above, in far higher percentages in the median pieces and grade off laterally. Chorda, hypophysis, suprarenal, gonad and spleen have occurred only in median grafts. Heart, liver and feather germs seem limited to lateral areas, *i. e.,* bilaterally located. The heart-forming area is quite elongated antero-posteriorly extending from a level just behind the anterior end of the process to a level 0.3 mm. to 0.4 mm. posterior to the primitive pit. At one certain part of this elongated area (posterior node level), however, heart tissue develops with greatest frequency (90%) and quantity and from here in both respects declines rather gradually anteriorly and sharply posteriorly (Fig. 1). The capacity to produce liver, although coinciding with the heart region, apparently does not extend so far posteriorly. The frequency of its formation is definitely lower than that of heart. The medio-lateral extent of the heart-liver area has not yet been definitely ascertained.

3. *Changes in the localization of areas with advance in development.* Certain evidence has accumulated which indicates strongly that the developmental potency within the various organ-forming areas, which extend like bands across the blastoderm at first, undergoes changes as development proceeds with consequent changes in shape of the area. We have already noted that the capacity to produce heart and liver tissue is confined to lateral areas at the head-process stage. Yet at an earlier stage (primitive-streak) the median pieces as well as the lateral have the power to produce both of these organ tissues.[2] Similarly, changes in thyroid-forming capacity occur which result in its loss from the median pieces at about the 2- or 3-somite stage.[3] In the case of eye, however, the

[2] Rudnick, D., *J. Exp. Zool.*, 1932, **62**, 287.

[3] Rudnick, D., *J. Exp. Zool.*, 1935, in press.

median portion of the blastoderm retains its eye-forming potency even later, *i. e.*, until approximately the 8-somite stage.[4]

4. *Characteristics of the organ-forming areas.* Each organ-forming area exhibits a gradient in developmental potency, the intensity of which gradually diminishes from the center peripherally until it completely disappears. These areas are then not definitely circumscribed and furthermore, the indefinite boundaries of adjacent ones overlap one another.

Areas lying transverse to the antero-posterior axis, *i. e.*, eye and mesonephros, exhibit a distinct asymmetrical organization—the right portion showing far less developmental potency than the left. The developmental potency which is invariably the highest in the median portion, usually falls off abruptly to the right and gradually to the left of the area (Fig. 1).

Although the present experiments were not designed to limit the boundaries of the various organ-forming areas, there are nevertheless, some definite indications that the shape or contour of each area is more or less characteristic of the organ system. In general it is somewhat elongated either in a transverse direction (eye, thyroid, lung epithelia, etc.) or in an antero-posterior direction (heart, mesonephros, etc.). The eye-forming area is thus far the only one which has been carefully mapped—its outline is eliptical (Clarke).

With advance in development the gradient in developmental potency originally characteristic of the area changes (apparently rapidly in some organ-forming systems and slowly in others) with the result that its shape becomes markedly altered. There is some evidence that the ultimate shape assumed by an area, just prior to the establishment of the organ rudiment, is in accordance with the configuration of the organ system to be formed.

[4] Clarke, L. F., *Anat. Rec.*, 1934, **58** (Sup.), 54.