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Appearance of Accessory "Organizers" in Overripe Eggs of the Frog.*

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The author has described¹ the condition of overripeness that develops in frog eggs if fertilization is delayed 3 to 5 days after ovulation. Among the abnormalities of embryonic development that follow, one of the most striking is the frequent appearance of reduplications. In the early gastrulation stage instead of the normal upper blastopore lip of limited extent and regular curvature there often appear long and irregular clefts and folds in the equatorial region. Attempts at gastrulation become visible not only on one side but all around the whole circumference of the embryo. As time progresses multiple blastopores and multiple gastrulation lead to the development of twin embryos. As we have pointed out previously,¹ this effect indicates that overripeness has brought about 2 concomitant changes in the embryos. First, the physiological correlations by which an embryo develops as a balanced organism are impaired. These correlations largely rest on inhibitory functions by which established "organizers" (inductors) suppress either the formation or the effective functioning of competing organizers. Secondly, "organizers" appear in lateral and ventral regions of embryos, where normally they never occur. We have described this as self-differentiation or merogenesis of physiologically isolated parts. The mechanism of this formation of secondary organizers remained a complete puzzle until the recent discovery of Holtfreter² that material from the ventral region of an early embryo which has no inductive qualities in living condition, acquires such potencies after being killed by heat, dryness, etc. We are inclined now to assume that the possibility to develop into organizer is inherent to any part of the embryo, probably even to every cell. The inhibitors that suppress their realization are destroyed by such factors as heat and dryness but also by the process of overripeness.

The accessory organizers induce characteristically different extra-embryos according to size and more lateral or ventral position.

* Aided by grants from the Elizabeth Thompson Science Fund.

¹ Witschi, Emil, *Verh. Natf. Ges. Basel*, 1922, **34**, 33; *Verh. Deutsche Zool. Ges.*, 1925, **30**, 91; *Proc. Soc. Exp. Biol. and Med.*, 1930, **27**, 475.

² Holtfreter, J., *Naturwissenschaften*, 1933, **21**, 766.

Mainly, however, is the final result determined by the degree of invagination during gastrulation. If an organizer is fully invaginated its apical end comes to lie near the animal pole of the egg and therefore in close proximity to the corresponding anterior end of the normal organizer. Ten cases of this type have been investigated. In every one a common dorso-ventral plane of symmetry has developed. A common heart is present and on the dorsal side the 2 neural tubes fuse either already in the cervical region or at least at the root of the common tail. The notochords always show the largest extent of duplication, often until near the end of the tail.

More interesting are over 20 cases of incomplete invagination. The anterior end may be found anywhere from the closing blastopore up to near the anterior pole. With the exception of the most rudimentary cases a separate heart forms anterior to the neural cord of the secondary embryo. A notochord of normal diameter is only present in embryos that possess a complete entodermal foregut, complete rhombencephalon, 2 ear vesicles and at least fragments of the mesencephalon. In several cases where the anterior pharynx is incomplete and only one ear vesicle present a notochord of reduced diameter has formed. If no ear vesicles are present and the foregut is more rudimentary, no notochord is ever found. This relationship is of interest because it proves that presumptive notochord is not definitely determined as notochord inducer unless it enters into certain relationships with other fields of differentiation near the anterior pole. From here the notochord inducer travels posteriorly like a rocket, leaving in its trail determined and immediately differentiating notochord material.

Unlike the notochord the neural primordium can start at any point. If invagination is very incomplete the secondary organizer becomes imbedded in the tailbud and may be carried subsequently back into the tail where merely a piece of tail-neural-tube is found, accompanied by some muscle fibers and an extra tail fin. Secondary neural tubes and secondary notochords may finally fuse with the corresponding primary structure though more often they remain completely separate. The diameter of the neural tube has no influence on the diameter of the notochord, and the fact that neural tubes in many instances develop in the absence of notochords proves that they are products of independent induction.