THE OCCURRENCE OF THE EVOCATOR IN ORGANISMS WHICH POSSESS NO NERVE CORD

BY C. H. WADDINGTON¹ AND A. WOLSKY, PH.D.

(Sub-department of Experimental Zoology, Cambridge.)

(Received October 5, 1935.)

THE active principle (the evocator) of the amphibian organisation centre is very widely distributed throughout the animal kingdom. We owe our knowledge of its occurrence mainly to the investigations of Holtfreter (1934), who systematically tested the inducing properties of tissues belonging to most of the main phyla, by the well-known technique of implanting them into the blastocoele of young newt gastrulae. Some of the tissues were poisonous to the gastrulae when they were implanted in the living state, but many of them could be rendered innocuous by a short immersion in boiling water. This treatment seemed in general to have little effect on the inducing properties of tissues which were non-poisonous in the living state, and it seems probable that the effect of the boiling on poisonous tissue has been to annul the deleterious effects of the implants rather than to alter their inducing properties. However, Holtfreter (1933) has also shown that in the ventral ectoderm and in the endoderm of the newt gastrula, the evocator exists in a masked form, so that these tissues have no inducing power until they have been killed; and we cannot be certain that a similar state of affairs is not found in those tissues which are too poisonous to be tested while still alive.

Holtfreter examined no animals lower in the scale of organisation than the worms, and thus all the animals with which he was concerned possess in their adult state some sort of nerve cord. Their tissues were all found to be capable of performing inductions, though there was some variation in "strength" of stimulus exerted by them. It is at least conceivable that the evocator which they are thus shown to contain has some function in their embryological development similar to that which is performed by the evocator in vertebrates. Prof. Kennaway suggested in conversation that it would be interesting to know whether the evocator occurs in animals which possess no nerve cord, and in which no inducing function could be suggested for it.

An investigation of this question was begun in the spring of 1934 during the visit of Dr Wolsky to this laboratory, using the coelenterate, *Hydra viridis*, as the animal to be tested. The living tissue was found to be extremely poisonous to *Triton* gastrulae, and the animals were therefore boiled in water for a short time $(\frac{1}{2}-1 \text{ min.})$ before being cut up and implanted into the blastocoele. This treatment entirely removed the poisonous properties of the tissue. Most of the implants

¹ Senior Student of the Royal Commissioners of the Exhibition of 1851.

Occurrence of the Evocator in Organisms which possess no Nerve Cord 93

induced extensive ectodermal thickenings, the cells of which in some cases assumed a more or less neural appearance. This probably represents a weak induction effect, and the thickenings would be classified as B + and B + + in the scheme used by Waddington, Needham, Nowinski and Lemberg (1935). The evidence of these thickenings seemed rather inconclusive, so a few more implantations were made during the spring of 1935. In this series one typical induced neural tube appeared. It demonstrates without question that the active evocator is present in dead *Hydra* tissue. No difference in activity has been found between the different parts of the *Hydra*, but no attempt has been made to undertake the extensive investigation which would be necessary to attack the question of whether there is a connection between the evocator content and the axial gradients of the animal.

Since this work was planned and performed, Fischer, Wehmeier and their collaborators (1935) have published a short note in which they claim that the stimulus to the development of neural tissue in the amphibian gastrula is given not by a definite evocator substance but by an evocating condition. This condition, they claim, is acidity ("Säurereiz"), which must, however, be provided by a liquid fatty acid or by an acid derived from the nucleo-proteins. This is not the place for a full discussion of this hypothesis, which will be criticised elsewhere on the basis of chemical investigations which are now in progress. It might be argued that the presence of the evocator in organisms with no nerve cord, where therefore no function can be plausibly suggested for it, would be easier to conceive of on teleological grounds if the evocating stimulus were provided by a general condition such as acidity rather than by a specific substance. It is doubtful whether much weight should be given to such considerations. In any case, many instances are known in which substances having a specific biological effect are remarkably widespread, occurring even in organisms where their effects cannot be manifested (e.g. oestrogenic substances in plants (Skarzynski, 1933)). It seems that a new step in evolution may involve the introduction not of a new stimulating substance, but rather of a new reaction to a substance already present.

There is one further point which must not be overlooked. We know, thanks to Holtfreter (1933), that the non-evocating parts of the amphibian gastrula become evocating when killed. We have as yet very little information as to what is involved in this activation of the evocator (but see Waddington, Needham and Brachet, 1935); it may depend on the liberation of the evocator from some inactive compound or on some alteration of the properties of the cell surface or on other reactions. But it must be pointed out that if some material could be found which, when implanted under the gastrula ectoderm, caused the activation of the evocator contained in that ectoderm, this material might be indistinguishable from the actual evocator itself. It is quite possible therefore that some of the animal tissues, such as the *Hydra* tissue dealt with here, or the acids employed by Fischer, Wehmeier and their collaborators, or the substances tested by Waddington, Needham and their collaborators, do not act by virtue of their own contained evocator but by reason of their capacity to activate the evocator contained in the ectoderm with which they are in contact. The investigation of this possibility must be the subject of future research.

SUMMARY.

1. Tissue from *Hydra viridis*, boiled in water for $\frac{1}{2}$ -1 min. and then implanted into the blastocoele of young newt gastrulae, evocates the formation of neural tissue, in the best cases of definite neural tubes.

2. Since Hydra possesses no nerve cord, the evocator which it contains cannot perform, during development, any function similar to that of the evocator in the amphibian egg.

3. It is pointed out that it would probably be impossible to distinguish between a substance which actually contained the evocator and one which could unmask the evocator which is known to be contained in the amphibian gastrula ectoderm. The substances and tissues which have hitherto been taken to be themselves evocating (including *Hydra* tissue) may therefore be agents which unmask the evocator already present.

REFERENCES.

- FISCHER F. G., WEHMEIER, E., LEHMANN, H., JÖHLING, L. and HULTZSCH, K. (1935). Ber. dtsch. chem. Ges. 68, 1196.
- HOLTFRETER, JOH. (1933). Roux Arch. Entw. Mech. Organ. 128, 584.
- ----- (1934). Roux Arch. Entw. Mech. Organ. 132, 307.
- SKARZYNSKI, B. (1933). Nature, Lond., 131, 766.
- WADDINGTON, C. H., NEEDHAM, J., NOWINSKI, W. W. and LEMBERG, R. (1935). Proc. roy. Soc. B, 117, 289.

WADDINGTON, C. H., NEEDHAM, J. and BRACHET, J. (1935). (In press.)