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Behavior in Amblystoma Larvae Lacking Forebrain, Eyes and Nasal Placodes.

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Observations have been made upon the feeding behavior in Amblystoma larvae devoid of the forebrain, eyes and nasal organs. The anlagen were removed from 60 embryos in Harrison's stage 21±,* in some experiments designed to study certain problems of morphogenesis of the brain. Since it was doubtful whether such individuals could lead an independent existence beyond the yolk resorption stage, 30 embryos were joined parabiotically with normal embryos to serve as nurses, as well as controls for the operated components. The remainder were allowed to develop as "free" individuals. Seventeen cases of parabiotic twins and 9 single individuals survived. In no case was there any external evidence of regeneration of the parts removed.

External malformations in the shape of the head resulting from the ablation are seen in Fig. 1 and 2. The growth of the lower jaw has apparently been unaffected, and is seen to protrude quite far beyond the upper jaw. A detailed study of the morphogenesis of the mid and hindbrain, in the absence of the hemispheres, will be made upon the operated components of the twins, using the brains of the normal components for comparison. A similar comparative study will be made also upon the development of the skull.

When the larvae had reached the feeding stage, 7 of the non-parabiosed individuals, despite the absence of the forebrain, eyes, and nasal organs, exhibited the capacity to feed upon daphnia and small enchytraeid worms. Like normal larvae, they exhibited snapping reactions when a needle, immersed in the water, was moved gently back and forth along side of the head. This capacity to sense moving objects, whether edible or not, bears out former observations,[1] that neither vision nor smell, nor both can be regarded as indispensable to the securing of food. We[1] showed that eyeless larvae, whether reared in light or darkness, grew as rapidly as their controls under similar conditions of feeding. Even when the receptor apparatus was restricted to the lateral-line sense organs, following removal of the eyes and nasal placodes, the growth in young larvae was not impeded. These findings supported the observations of Sharrer[2] who showed that eyeless larvae would snap at minute streams of water directed towards the side of the head. If, however, the primordia of the lateral-line organs were removed from one side, the larvae would snap only if the stimulus were applied to the unoperated side.

Nicholas,[3] who removed the eyes of *A. tigrinum* embryos, claimed that the larvae failed to respond positively to moving objects which did not stimulate the olfactory apparatus. He thus regarded the olfactory apparatus as paramount in obtaining food when the visual sense is obliterated, yet he also recognized that following ablation of both the eyes and nasal organs, the animals were capable of snapping at moving objects, whether edible or not. Previous to the observations of Nicholas, Burr[4] had emphasized the importance of smell, especially after removal of the eyes.

Since the lateral-line sense organs are sufficient for sensing food, the question naturally arises whether, in normal larvae, these organs play a significant role in this capacity.

Food sufficient for *normal* growth, in larval stages can be located by the lateral-line organs alone, but only if the forebrain is in-

* In stage 21, the medullary folds are completely fused.

1 Detwiler, S. R., and Copenhaver, W. M., *Anat. Rec.*, 1940, **76**, 241.

2 Sharrer, E., *J. Exp. Zool.*, 1932, **61**, 109.

3 Nicholas, J. S., *J. Exp. Zool.*, 1922, **35**, 257.

4 Burr, H. S., *J. Exp. Zool.*, 1916, **20**, 27.

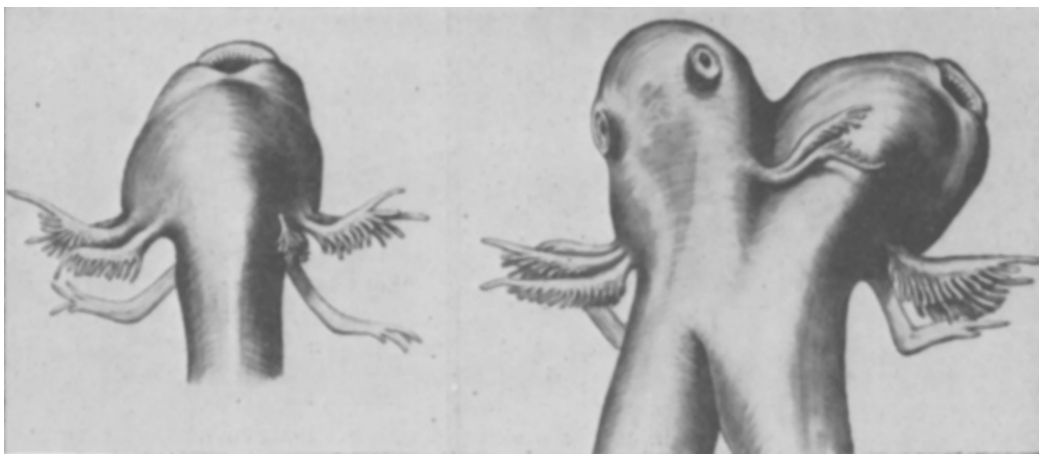

FIG. 1. FIG. 2.

FIG. 1.
Drawing of the case FBEB 44, lacking forebrain, eyes, and nasal organs. 26 days after operation. × 8.

FIG. 2.
Drawing of case FBEB(P) 20, the right component of the parabiotic twin lacks the forebrain, eyes, and nasal organs. The left component is normal. 26 days after operation. × 8.

tact. Larvae lacking the hemispheres are capable of feeding, but their intake is much less and their growth is markedly curtailed. Spontaneous behavior in general is greatly reduced, both quantitatively and qualitatively, especially the foraging activities, regardless of the amount of food available. The lengths of the larvae at 45 days of age are slightly more than 50% of the length of maximally fed normal larvae of similar age.

Nicholas[5] excised the embryonic mesencephalon and replaced it with a limb and pronephric rudiment. Such animals were unable to feed, and he regarded this failure as due to a *block* in the nervous system brought about by mesencephalonectomy. It would appear that if the presence of the mesencephalon is essential, it acts as a coordinator of motor activities rather than serving as a *bridge* between forebrain and medulla, for the present experiments demonstrate that larvae lacking hemispheres are capable of carrying out all activities necessary for obtaining food.

[5] Nicholas, J. S., *J. Exp. Zool.*, 1930, **55**, 1.

The operated components of the parabiotic twins were also seen to snap and engulf food, but in these cases, the eating function was taken over largely by the more active conjoined normal components. Consequently, the growth rate of the twins was greater than in the operated free individuals, but not as great as in normal animals.

Summary. Amblystoma larvae, deprived of the cerebral hemispheres, eyes, and nasal organs react by snapping at inanimate objects in motion. They are capable of feeding upon daphnia and small enchytraeid worms. Their food intake and growth is greatly reduced as compared with these functions in larvae lacking eyes and nasal organs, but with the hemispheres intact.

The lateral-line sense organs alone constitute an adequate receptor apparatus for the detection of food in motion. The motor activities concerned with lurching, engulfing food, chewing and swallowing are carried out in a normal integrated manner, although they are less vigorous than in larvae with intact hemispheres.