The origin of Mauthner's cells in fundulus heteroclitus embryos

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THE ORIGIN OF MAUTHEIN'S CELLS
IN
FUNDULUS HETEROCLOITUS EMBRYOS

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CHAPTER I

INTRODUCTION

Mauthner's cells, two huge neurones, occurring in the central nervous system of teleosts and amphibians have commanded considerable interest because of certain constant anatomical features. The cell body in the adult is approximately 66 x 63 x 60 microns, the dendritic connections are very extensive and the cell occupies a characteristic position in the medulla.

Because of the relation, in the adult, of Mauthner's cell and fibers with other tracts and nuclei of known function, I propose in this experiment to study the appearance of Mauthner's cell in Fundulus heteroclitus embryos, in particular its position in the brain stem and the differentiation of its fibrillar elements.
CHAPTER II

HISTORICAL REVIEW

According to Bartelmez (1915) in his work on the adult trout and salmon, the Mauthner's cell body lies just rostral to the genu of the seventh nerve at the caudal end of the cerebellar peduncle. It is bent at approximately a right angle in the middle with the lateral limb directed caudally and the ventral limb rostrally. The axon arises medially from the apex of the angle, decussates with the axon of the opposite side and turns abruptly caudally to descend in the cord in close proximity with the medial longitudinal fasciculus giving off collaterals to the motor nuclei.

There are in typical forms two large dendrites, the lateral and ventral. Bartelmez describes the lateral dendrite as extending almost to the lateral periphery of the oblongata and being enveloped in a sheath of thick eighth root fibers which end in club-like expansions upon its surface. There is no evidence of fusion between the dendrite and fibers, the two are merely in contact. Impulses entering this dendrite then, are largely from the vestibular nerve and are equilibratory in nature. Most teleosts have but one single large ventral dendrite; however in Amerius, Bartelmez describes another which he calls the inferior ventral dendrite, branching in the medial longitudinal fasciculus. Bartelmez gives a probable explanation of its existence in the follow manner:
When in hypertrophy of the gustatory system the ventral acoustic nuclei were crowded caudally and so separated from Mauthner's cell, the superior ventral dendrite retained its position because of its intimate relation to the chief fifth nucleus and cerebellum, while the inferior dendrite was developed to receive the impulses from the ventral eighth nuclei.¹

The superior ventral dendrite extends slightly rostrally receiving its chief impulses from the chief fifth nucleus, the tectum through crossed and uncrossed tecto-bulbar tracts and from the cerebellum by way of the indirect cerebello-tegmental system. In addition to the superior and inferior ventral dendrites there are small dendrites arising from the ventral aspect of the cell body and branching into the lateral longitudinal fasciculus.

The axon cap was so called by Bartelmez (1915) because it fits like a cap over the region of the axon hillock and the adjoining medial surface of the cell. The axon passes straight through the middle of the cap. It also extends over the root of the superior ventral dendrite, but does not reach the lateral dendrite. The cap is composed of three kinds of fibers which are: (a) Collaterals from neighboring fibers; (b) minute dendrites from the underlying region of the cell body, and (c) supporting elements. The collaterals are fibers from the medial longitudinal fasciculus, fibers from the secondary acoustico-lateral tract,

¹ George W. Bartelmez, "Mauthner's cell and the Nucleus Motorius Tegmenti", Journal of Comparative Neurology, XXV (1915), 87.
and fibers of the eighth root crossed and uncrossed. The
dendrites of the cap receive stimuli that do not end on
the cell body proper. The other elements of the cap are
said to be supporting elements and not nervous elements
because they contain no Nissl substance, the size does not
correspond to other nerve elements associated with the cell,
the cell anastomose with one another, the nucleus shows
two nucleoli, there's evidences of amitoses and the fibers
are identical with those of neuroglia.

The nucleus of the cell contains one prominent nucleolus.
The Nissl substance is distributed evenly throughout the
cell body and at the base of the dendrites. It appears in
the form of flakes arranged in rows more or less parallel
to the surface. According to Harui (1918) the neurofibrils
run in a straight or winding fashion through the cell body
and generally parallel to the axis of the cell. The fibers
bifurcate but never anastomose to form a net. About the
Golgi net Harui states:

Careful investigation of the synapse of this giant
cell by means of different methods revealed a most charac-
teristic net-work, which covers the cell-body as well
as its processes like a basket and also fills the axon
cap. There is no doubt that this net-work is identified
with the structure, which was described for the first
time by Golgi ('93) and later called the Golgi net by Bethe.

K. Harui, "On the Finer Structures of the Synapse of
Mauthner's Cells, with especial reference to 'Golgi Net'
of Bethe, nervous pericellular terminal not of Held. Jour-
nal of Comparative Neurology, XXX (1918), 127.
Bartelmez cites seven types of impulses that may enter a single Haueter's cell as follows: homolateral and contralateral vestibular root fibers ending on the lateral dendrite, axon cap and pericellular net; external and internal arcuate fibers from the ventral acoustic nucleus ending in the pericellular net fibers from the medial longitudinal fasciculus ending in the axon cap; cerebello-tegmental fibers ending in the pericellular net of the superior ventral dendrite; collaterals from the crossed and uncrossed tegmento-bulbar tracts to both ventral dendrites; and fibers from the principle trigeminal to the pericellular net of the superior dendrite.

Detwiler (1927) states that there are only a few differences between the Haueter's cell in Amblystoma and in the teleosts as described by Bartelmez; those differences deal mainly with the dendrites and their connections. In contrast to the two ventral dendrites as described by Bartelmez, according to Detwiler there is only one huge ventral one in Amblystoma. Another difference is seen in the branching of the lateral dendrites. The chief branching in teleosts is among the eighth root fibers and the cells of Dieter's nucleus; whereas in Amblystoma it spreads throughout the distribution area of all the lateral-line roots, and shorter processes arising from the cell body extend outward among the entering fibers of the eighth root.
CHAPTER III

MATERIALS AND METHODS

There were two types of materials used. Fundulus heteroclitus embryos in Oppenheimer stages 22, 2½, and 26 obtained from the Marine Biological Laboratory at Woods Hole, Massachusetts, and a few trout embryos fifty-five days old obtained from the Fishery in Walhalla, South Carolina. This material was available at no extra cost, therefore, a few embryos were sectioned for comparison.

Since the old protargol is off the market there was a problem of which stain was best for embryonic nervous tissue in those particular stages. Table I (p. 3) shows the results of a number of stains following the various fixatives. In addition to the above material some Fundulus heteroclitus previously fixed in modified Bouin were re-fixed.

With the Protargol-S stain Bodian Protargol method (1947, p. 102-23) was followed with two variations: no copper was used and protargol-S was substituted for the regular protargol. There were no variations on the Two-Hour-Protargol method according to Davenport, McArthur and Bruesch (1947, p. 102-24) slides stained with toluidin blue were left overnight in the following solution:

- 10cc. of 0.5% lithium carbonate
- 100cc. of 1% toluidin blue

The slides were differentiated in 70% alcohol and after
dehydration to 95% alcohol were counterstained in eosin. Embryos stained in thionin were placed overnight in a saturated solution of thionin in a 1% aqueous solution of carabolic acid, differentiated in 70% alcohol and counterstained with eosin. Stock embryos were kept in 70% alcohol solution in glass vials. Those to be used were transferred to Syracuse watch crystals and placed under the binocular dissecting microscope. Using forceps, the yolk was clamped with one pair while with the other pair a tear was made in the tough egg membrane by pulling and causing excessive tension. From the torn point the membrane was peeled off leaving the embryo exposed. Clamping the yolk material with one pair of forceps and replacing the pair in the right hand with a spear-point dissecting needle, the embryo was loosened from the underlying yolk material and placed in a seventy per cent alcohol solution. The embryos were then run through a process of dehydration and infiltration. Alcohols were used for dehydration, oil of bergamot for the clearing agent and paraffin for infiltration and embedding. Because of the small size of the embryo the whole process of dehydration, infiltration and embedding could be done within twelve hours. The embryos were placed on a cutting block, trimmed and sectioned at seven microns. After the ribbons were affixed to slides they were placed in a box to dry for a period of from one to one and a half weeks.
<table>
<thead>
<tr>
<th>SPECIMEN</th>
<th>FIXATIVE</th>
<th>STAIN</th>
<th>RESULT</th>
</tr>
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<tbody>
<tr>
<td>Re-fixed Fundulus heteroclitis</td>
<td>Protargol-S</td>
<td>Protargol-S</td>
<td>-</td>
</tr>
<tr>
<td>Re-fixed <em>P.</em> heteroclitus</td>
<td>2 hr. Protargol</td>
<td>2 hr. Protargol</td>
<td>-</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>Bouin</td>
<td>Protargol-S</td>
<td>±</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>Modified Bouin</td>
<td>Protargol-S</td>
<td>±</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>Protargol-S</td>
<td>Protargol-S</td>
<td>±</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>2 hr. Protargol</td>
<td>2 hr. Protargol</td>
<td>±</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>Bouin</td>
<td>2 hr. Protargol</td>
<td>±</td>
</tr>
<tr>
<td>Trout embryo</td>
<td>Mod. Bouin</td>
<td>2 hr. Protargol</td>
<td>±</td>
</tr>
<tr>
<td><em>F.</em> heteroclitus</td>
<td>Stockard</td>
<td>2 hr. Protargol</td>
<td>+</td>
</tr>
<tr>
<td><em>F.</em> heteroclitus</td>
<td>Stockard</td>
<td>Thionin Eosin</td>
<td>+</td>
</tr>
<tr>
<td><em>F.</em> heteroclitus</td>
<td>Stockard</td>
<td>Toluidin blue Eosin</td>
<td>-</td>
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*+ Indicates good cellular detail*

*± Indicates fair stain*

*- Indicates no cellular detail*
CHAPTER IV

RESULTS

In Fundulus heteroclitus embryos Mauthner's cell stood out very distinctly in stages 2½ and 26. They can very easily be identified by the high degree of differentiation in contrast to the surrounding cells of the same region. These cells are beginning to elaborate neurofibrils which begin to push out and form broad expansions, which will form the axon and dendrites of the cell.

There are two embryos (Table II) in stage 22 with Mauthner's cells present. Even in these two embryos there is a difference in the appearance of Mauthner's cell. In one embryo (2E Fig. 1) differentiation is manifest in the presence of neurofibrils, whereas in the other (22M Fig. 2) they cannot be clearly distinguished. Even in 22M, however there is no doubt that the cell is Mauthner's cell because, among other characteristics, it exhibits a high degree of susceptibility to stains in contrast to the almost negative staining reaction of the surrounding embryonic nerve cells. It is probable that these two embryos are in a later stage than the other embryos of stage 22 or that they are in stage 23. I say this because the remaining embryos of stage 22 show no definite Mauthner's cell. The cells of the brain stem of an embryo in stage 22 show a variety of sizes and shapes (Fig. #3), consequently it is practically impossible to find one cell on each side of the embryo and at the same
position with similar characteristics.

A comparison of the figures in Table II with figures 2, 4, and 5 shows that actual growth rate of the perikaryon is slower than the rapid differentiation rate (elaboration of neurofibrils). In stage 22 (Fig. 2) the neurofibrils have not begun to make their appearance. The cytoplasm stains evenly. In stage 24 and 26 the cytoplasm appears to contain small dots scattered throughout. This dotted effect is due to the fact that the neurofibrils were cut across their horizontal plane.

In both embryos of stage 22 Mauthner's cell lies in a ventro-lateral position in the medulla in the region of the otocyst. The migration of the cell cephalad or caudad is negligible with respect to its medial migration. In stages 25 and 26 there is evidence of either a medial migration or displacement of the cell due to the accumulation of developing fiber tracts.

None of the cell bodies are present in more than two sections so that they could not exceed 1½ microns in their cephalo-caudal plane.
### TABLE II

**MEASUREMENTS OF MAUTHNER'S CELLS**

<table>
<thead>
<tr>
<th>SPECIMEN</th>
<th>STAGE</th>
<th>RIGHT PERIKARYON size in micra</th>
<th>LEFT PERIKARYON size in micra</th>
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<tr>
<td>2M</td>
<td>22</td>
<td>7.66 x 4.99</td>
<td>7.99 x 4.99</td>
</tr>
<tr>
<td>2E</td>
<td>22</td>
<td>6.99 x 5.66</td>
<td>6.99 x 5.66</td>
</tr>
<tr>
<td>2l, A1</td>
<td>2l</td>
<td>7.33 x 6.66</td>
<td>*9.10 x 4.20</td>
</tr>
<tr>
<td>2l, D2</td>
<td>2l</td>
<td>7.33 x 6.66</td>
<td>7.33 x 6.20</td>
</tr>
<tr>
<td>2l, E1</td>
<td>2l</td>
<td>7.66 x 7.33</td>
<td>6.20 x 5.33</td>
</tr>
<tr>
<td>hL-2</td>
<td>2l</td>
<td>6.66 x 7.33</td>
<td>7.20 x 6.66</td>
</tr>
<tr>
<td>hR</td>
<td>2l</td>
<td>*9.65 x 5.33</td>
<td>*9.10 x 4.20</td>
</tr>
<tr>
<td>hG</td>
<td>2l</td>
<td>7.33 x 6.66</td>
<td>7.33 x 6.20</td>
</tr>
<tr>
<td>hF</td>
<td>2l</td>
<td>10.00 x 6.70</td>
<td>10.00 x 6.66</td>
</tr>
<tr>
<td>6P</td>
<td>26</td>
<td>10.00 x 6.70</td>
<td>10.00 x 6.70</td>
</tr>
<tr>
<td>26A</td>
<td>26</td>
<td>10.00 x 6.66</td>
<td>10.00 x 6.70</td>
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<tr>
<td>6G</td>
<td>26</td>
<td>10.00 x 6.66</td>
<td>10.00 x 6.70</td>
</tr>
<tr>
<td>26G-3</td>
<td>26</td>
<td>10.65 x 7.66</td>
<td>11.00 x 7.66</td>
</tr>
<tr>
<td>6F</td>
<td>26</td>
<td>11.32 x 7.99</td>
<td>11.00 x 7.66</td>
</tr>
<tr>
<td>26L</td>
<td>26</td>
<td>9.20 x 6.20</td>
<td>10.22 x 7.33</td>
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**STAGE**

<table>
<thead>
<tr>
<th>AVERAGE SIZE in micra</th>
</tr>
</thead>
<tbody>
<tr>
<td>22</td>
</tr>
<tr>
<td>2l</td>
</tr>
<tr>
<td>26</td>
</tr>
</tbody>
</table>

*These cells were more oblong than the other cells. It is probably the result of improper sectioning rather than a characteristic of the cell.*
The absence of some measurements in Table II was caused by the orientation of the embryo on the cutting block. Some sections did not pass through the center of the perikaryon, thereby making measurements of that particular cell impossible.
CHAPTER V

DISCUSSION

During Hertwig's time, before the histogenesis of nerve tissue was fully understood, it was thought that the protoplasmic outgrowths seen around nerve cells were undifferentiated protoplasmic threads and that these threads were utilized as paths by the growing axons. Neal (1921) having observed the outgrowth of motor neurons and their connection with the musculature disproved this theory. He maintained that the primary connections between nerve and muscle were nervous outgrowths and not merely indifferent protoplasmic threads. Harrison (1921, p. 129) in his work on the developing neuroblasts in Amphibia gave the following detailed description of its development:

The cells of the medullary cord stretch out radially, and many of them now reach from the inner to the outer limiting membrane. The nuclei are likewise elongated, certain cells, however, occupying the peripheral zone of the wall of the tube, remain rounded and contain round nuclei. These are the first of the neuroblasts of His which will soon begin to form nerve fibers.¹

Harrison further stated that there are two separate processes involved in nerve development. First there is protoplasmic movement which results in the drawing out of a part of the neuroblast into a thread of protoplasm, the primitive nerve

¹ Ross C. Harrison, "The Outgrowth of the Nerve Fiber as a Mode of Protoplasmic Movement" Journal of Experimental Zoology, IX (1910), 787.
fiber; and secondly the differentiation of this protoplasm by the formation within it of neurofibrillar substance.

Coghill (1924) having correlated the anatomical and physiological studies of the growth of the nervous system in Amphibia, followed the differentiation of the neuroblasts of the floor plate of animals in the non-motile stage. He found that the first evidence of differentiation is the presence of intracellular fibrillae. These fibrillae extend throughout the cell and finally extend from the cell as a fibrillar process. At first the process extends in only one direction, then with advancing differentiation the process appears on the other side of the cell. The highest degree of differentiation in the non-motile stage is found in the regions of the fifth, seventh and eighth cranial roots. At this time there are still no structures that can be regarded as a functional commissure. He states:

It is certain, therefore that nervous conduction in cells is correlated with a system of protoplasmic fibrils throughout the entire extent of the cell.\(^1\)

Comparing then, Mauthner's cell in the successive stages of the developing Fundulus heteroclitus embryo, there is little doubt that the earliest stages of differentiation

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\(^1\) George Coghill, "The Floor Plate of Amblystoma" Journal of Comparative Neurology, XXXVII (1924), 37.
are represented here.

Youngstrom (1940) working with Amblystoma sets up two distinct systems of somatic motor innervations. The first one to appear he calls the primary system and the one that arises secondly he calls the secondary system. The primary system is present in the early developing stages, thereby controlling the general pattern of behavior of the organism. With the development of specialized organs comes the elaboration of a special set of ventral root fibers. Concerning this secondary system Youngstrom states:

Observations reported herewith indicate that a new motor system appears pari passu with the development of the independent withdrawal reflex in the limbs. From the order of its development this system has been called secondary. It has been found to exist side by side with the primary motor system constituting a double motor innervation of skeletal muscle... Even in the adult of Amblystoma the primary motor component is by far the most conspicuous constituent of the ventral roots.¹

If such a set of systems do exist there is no doubt that Mauthner's cell, by its early appearance in development would belong to the primary motor system.

There exists even yet, some doubt as to the specific role of Mauthner's cell in the motor reflex pattern. Fibers of the reticular elements which are concerned particularly with the coordination of motor reflexes run along

¹ Karl Youngstrom, "A Primary and Secondary Somatic Motor Innervation in Amblystoma" Journal of Comparative Neurology, LXXIII (1940), 139.
with Mauthner's fibers, in the adult as far as the termination of Mauthner's fibers around the motor nuclei for the tail region. This would seem to indicate that the cell is of great importance in the preservation of equilibrium and such acts necessary to maintain equilibrium that involve movements of the tail. On the other hand Coghill (1926) postulated that in young embryonic fish and amphibian Mauthner's cell fiber, which is an important element of the fasciculus longitudinalis medialis is probably not yet functional, for even though the dendrites have grown completely across the motor and sensory tracts, their axons could not be identified in decussation or in the tract.

At about the same time, Detwiler (1926-27) experimentally removed that part of the medulla containing Mauthner's cell and studied the effect of the absence of one neuron upon the activity of Fundulus heteroclitus. He found that the animals lacking Mauthner's cell fell into two behavioral groups. In one equilibratory disturbances were either slight or entirely absent but the animals always exhibited "jerky" swimming. They were rapidly exhausted and unable to execute the normal sustained rapid swimming reflexes. In the other group the functional disturbances were essentially like those animals lacking an ear vesicle; the head was bent toward the opposite side, body torsion was present, there was a marked flexion of the forelimb on the operated side and extension of limb on the opposite side, the ani-
mal exhibited corkscrew swimming and it came to rest in almost any position. In one of the cases when the operation was not complete, in that Mauthner's cell was not removed, the jerky swimming was not noted. Detwiler interpreted the facts as meaning that the type of response elicited by the lack of Mauthner's fiber suggested that the giant neuron plays an important role in transmitting impulses which are concerned in sustained coordinated rapid reflexes.

At 55 days the trout embryo has already hatched, but is very inactive due to the large quantity of yolk material that still exists. *Fundulus heteroclitus* hatches at stage 32 and becomes active immediately. The swimming reflex is certainly one of the first that those fish which become immediately after hatching exhibit. Comparing Mauthner's cell in stage 26 of *Fundulus heteroclitus* and the cell on the 55th day trout embryo shows that the rate of specialization in the trout is lower than in *Fundulus heteroclitus*. A possible explanation may be that since the trout is inactive at the hatching stage and since *Fundulus heteroclitus* is very active, *Fundulus* utilizes Mauthner's cell in its early swimming reflexes.
CHAPTER VI

SUMMARY

With the staining techniques used, the differentiating Mauthner's cell is not recognizable in the typical stage 22 of the developing Fundulus heteroclitus embryos. Because of the elaboration of neurofibrils and positive staining reaction, Mauthner's cell is easily recognized in stages 23 and 26.

The rate of differentiation of Mauthner's cell is higher than the growth rate.

The Mauthner's cells pictured here represent successive stages in the elaboration of the neurofibrillar elements.
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Green, W.F. and Henry Laurens 1923 Extirpation of eye and ear in Amblystoma embryos. Am. J. Physiol., vol. 64, p. 120.


Figure 1. Mauthner's cell from stage 22 of Fundulus heteroclitus embryo.

Figure 2. Mauthner's cell from stage 22 of Fundulus heteroclitus embryo showing less specialization than figure 1.

Figure 4. Mauthner's cell from stage 24 of Fundulus heteroclitus embryo.

Figure 5. Mauthner's cell from stage 26 of Fundulus heteroclitus embryo.

Figure 6. Mauthner's cell from 55 day old trout embryo.
Figure 3. Section through hindbrain of Fundulus heteroclitus in stage 22 showing variety of size and shape of cells.
Fig 7. Section through medulla of *Fundulus heteroclitus* in stage 214 to show position of Mauthner's cell. The cell occupies a ventro-lateral position on the left side.
Figure 3. Section through medulla of *Fundulus heteroclitus* in stage 26 to show position of Mauthner’s cell. Cell occupies a more medial position in contrast to lateral position in figure 7.