THE EFFECTS OF FOREBRAIN LESIONS ON THE AGONISTIC BEHAVIOR OF THE BLUE GOURAMI, TRICHOGASTER TRICHOPTERUS (PALLAS)

By

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1970

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
July, 1973

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ACKNOWLEDGEMENT

Thanks are due Drs. R. J. Miller, M. R. Curd, and W. A. Drew who served on my committee. I would also like to express my thanks to Dr. R. W. McNew, who acted as statistical advisor for the study.

My thanks also go to Mr. A. Jearld Jr., who helped record the data, and Mr. C. W. Houston, who helped record and transcribe the data.

Finally, I am grateful to Miss E. A. Mawdsley, who helped type the rough draft.

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CHAPTER I

INTRODUCTION

Study of the brain of fishes began in the later 1800's with anatomical studies of the entire structure. However, knowledge of the fish brain has not been intensively pursued until recently, particularly since the mid-1950's. This was mainly because the teleost brain develops by eversion instead of evagination and thus is divergent from the general line of evolution leading to the mammalian brain. This point has been generally accepted since the publication of Ariens Kappers, Huber and Crosby's text, Comparative Anatomy of the Nervous System of Vertebrates, Including Man, in 1936 and Herrick's (1922) earlier paper. Since the majority of investigators were interested in the evolution of the mammalian brain, research on the teleost brain did not seem worthwhile to them.

Aronson (1967) points out that the olfactory nerve terminates solely in the forebrain which must, therefore, be the primary integrative center of olfaction. He raises questions on the relationships between olfactory and cognitive processes and how these relationships have developed through millions of years of evolution. Savage (1968) has stated on the basis of Sherrington's (1906) work that "odors signifying prey would be analysed by the forebrain and the rest of the system /would be/ alerted by that area. . ." This, he believes, is the basis for Aronson's (1963) theory that the function of the teleost forebrain is primarily arousal. This statement is not accurate, however, since most fish are not predators and all other sensory modalities have input into the forebrain with no evidence that olfaction was necessarily the first to have had connections there.

There is considerable recent evidence for some convergent evolution, and homologies have been postulated among many structures in the complex teleostean forebrain and mammalian forebrains (Schnitzlein, 1968, Drooglever Fortuyn, 1961). Most investigators are more conservative, preferring to use more topographical nomenclature, and await further research in the area before stating definite homologies. Aronson (1967) puts it more succinctly, ". . .there is considerable morphological evidence that all major forebrain areas are present in teleosts, but as a result of the peculiar process of eversion and the obliteration of the lateral ventricles, exact homologies of the different pallial and subpallial areas are not clear and the terminology is varied."

Appendix A is an outline of the nomenclature used by early workers as presented by Ariens Kappers, Huber and Crosby (1936), and shows how Hale (1956a,b) arrived at his synthesis of the nomenclature (see column 6, Appendix A). Only areas of major differences are given.

Appendix B shows the more recent and divergent nomenclatures and their proponents. Topographical nomenclatures appear at the right side, while investigators who prefer to use homologous nomenclature comparing the fish brain to the mammalian brain appear on the left, with some intermediate schemes between the extremes. Nomenclature used in this paper follows the topographical point of view.

Historically there have been three basic results of research on behavioral effects of forebrain lesions in fish: (1) no changes in locomotion, balance, orientation, and feeding; (2) specific changes in behavior such as changes in social behavior, sexual behavior, schooling, sensory discrimination, and classical and instrumental conditioning; (3) a loss of initiative or responsiveness; a lack of alertness.

Most of the very early workers noted no specific changes in balance, locomotion, feeding or orientation after forebrain ablation. This was reiterated as late as 1939 by Meader for *Holocentrus*, Aronson (1948) for *Tilapia*, and Kamrin and Aronson (1954) for *Xiphophorus*. Hale (1956b) reported similar results, but found changes in other areas of performance in *Lepomis*.

In the early thirties many investigators began to find subtle changes in behavior after forebrain extirpation. These changes occurred primarily in schooling ability, learning ability, reproductive behavior, and aggressive behavior. Kumakura (1928), Noble (1936), and Wiebalck (1937) found an inability in various species of fish to school after forebrain ablation. Another change was noted by Koshtoiants, Maliukina and Aleksandriuk (1960), who found a reduction in the "group effect: of oxygen consumption in schooling fish. Hale (1956b) and Warren (1961) found maze running and problem solving ability significantly lower in ablated fish. Evidence that learning ability was impaired was given by Bernstein (1961 a,b), who found that ablated goldfish were able to make brightness, but not hue, discriminations in a classical conditioning situation. Savage (1968) reported retention and relearning were drastically impaired by forebrain removal in fish.

He also found a shortened latency to an escape stimulus in a shock-box situation, which was in contrast to Aronson and Kaplan (1967) who found an increased latency to respond in a similar situation. Segaar (1960) found forebrain ablated Gasterosteus to be significantly inferior to controls, in ability to learn and retain various types of avoidance responses. Schonherr (1955) found male sticklebacks were unable to build nests and were less aggressive after forebrain ablation. Segaar (1961) and Segaar and Nieuwenhuys (1963) verified this and also found changes in parental care given Gasterosteus fry. Kamrin and Aronson (1954) found no mating behaviors abolished in Tilapia, but a lowered responsiveness to the partner in mating bouts. Noble (1936), using several species, found an inability to properly care for fry. Marked changes in agonistic tendencies have been noted after ablation. Schonherr (1955), Segaar (1960, 1961), and Noble and Borne (1941) found that bilateral extirpation altered agonistic patterns in many species, but the latter authors found no such impairment in Xiphophorus.

Many investigators have reported only a general loss of responsiveness with forebrain ablation. Vulpian (1866), Janzen (1933), Hosch (1936), and Hale (1956a) reported normal agonistic bouts, but latency to the bout was greatly increased. Aronson and Heberman (1960) reported a high latency for movements and a high variability in those latencies. Janzen (1933) and Hosch (1936) reported a lack of initiative and very regular opercular movements in their forebrainless fish. They also reported a lowering of the fishes' general activity level. Noble (1937, 1939), Schonherr (1955) and Segaar (1960, 1961) found a failure to coordinate, and defects in orientation in their ablated fish. Ingle (1965) found his fish "static" with what he called, ". . . a lack of error-making ability."

The purpose of the present study was to examine the effects on agonistic behavior in blue gouramis of ablating some of the specific brain areas found by earlier authors to affect behaviors, and to test the general arousal hypothesis postulated by several authors. Many of the earlier investigators used fewer than twenty-five fish in their studies and few reported detailed quantitative data on behavior. Few investigators did histological studies on their lesioned subjects but relied heavily on visual observation of the lesions. Many studies took place over a long period of time and regeneration of tissue may have taken place. Aronson (1967) found that the grouping of tests and length of testing periods made some difference in performance, with operants approaching normal levels of learning after longer testing soon after lesioning.

Six different preparations were made, with twenty-one specimens of each preparation, and their behavior in dyadic agonistic encounters involving each preparation against themselves and each of the other five preparations were recorded on an event recorder. Following the encounter, the brains of the fish were removed and a tissue study done to determine that the desired forebrain areas had been ablated. The data analysis which followed, although not statistically significant due to the high variability of the behavior of the fish, indicated that some behavioral changes were caused by the ablation of certain areas of blue gourami forebrain.

CHAPTER II

MATERIALS AND METHODS

Blue gourami, Trichogaster trichopterus, a perciform fish of the suborder Anabantoidei was chosen for this study for several reasons. It is characterized by the presence of a suprabranchial accessory respiratory apparatus, known as the labyrinth organ, which allows the use of atmospheric oxygen by the fish and enables the fish to remain out of water for several hours provided its skin remains moist. The agonistic behavior of T. trichopterus is well known and documented (Miller, 1964; Miller and Miller, 1969: Frey, 1970), so a preliminary study to determine behavioral units of the species was not necessary. Finally, as in many adult fishes, the brain is sufficiently smaller than the cranium to provide adequate space to permit the tip of a drill bit to penetrate the skull bones without damaging the brain. To reduce the number of variables in the study, only males were used.

The fish were first removed from their community tank in small groups and isolated individually for ten days in an attempt to negate possible effects of prior experience. They were placed in identical white plastic buckets of water, to which they were returned post-operatively. The fish received a typical daily diet of flake fish food which was supplemented with live daphnia once a week. The standard length of the fish was recorded at the time of isolation and fish with standard lengths within two millimeters of one another were paired for the operations and bouts.

Paired operations were then performed in random order under a binocular microscope with the fish held immobile for the operation by an apparatus of sponge and plaster of Paris. The plaster of Paris portion was formed by impressing a large, preserved specimen in wet plaster. The areas near the operculum were hollowed to allow free gill movement, and a portion of a bent paper clip was inserted anteriorly in such a position that it would fit over the upper jaw of the fish, thus preventing sideways movement of the head. While the plaster of Paris was still wet, long, thin strips of sponge were pressed into the areas formed by the ventrum of the preserved specimen to protect the bodies of the treated fish from abrasion by the plaster. In the course of operation, the part of the fish posterior to the operculum was held stationary by two large damp sponges wedged on each side of the fish and held in place by elastic bands. All sponges were kept damp when in use, as was the body of the fish while held in the immobilizer (see Figure 1 for apparatus).

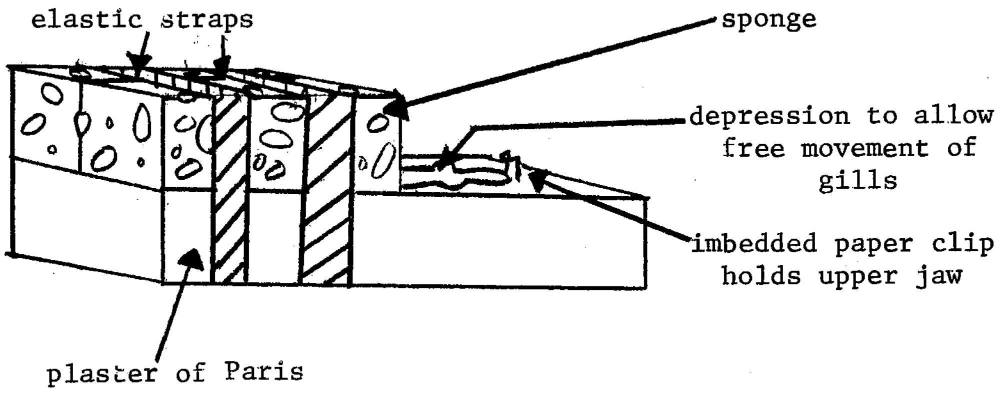

Figure 1. Immobilizer

Six operative procedure were used. The first "operation" involved no operation and was, in fact, a normal fish used as one type of control for the experiment. A second control was treatment two which consisted of opening, then closing the skull while leaving the brain undisturbed. For operation three, lateral ablations were made in order to remove the lateral and dorso-lateral nuclei; Noble (1936) found similar ablations to cause a lack of coordination in breeding and care of young in Cichlids. In treatment four, central and medial ablations were made. This involved removal of the pars dorsalis and pars medialis of the dorsal olfactory area and posterior parts of the nucleus posterior commissuralis. The fifth procedure was a complete unilateral extirpation with alternate sides removed each successive time the operation was performed. The final procedure involved total bilateral extirpation except for the small ventro-posterior area which is overhung by the optic tectum. Noble and Borne (1941) found this ablation reduced the level of aggressive activity in several species.

Initially, small skull opening the size of the drill bits were made using drill bits of sizes ½ round 310, and 1 square 558. Designated areas of the brain were then removed by using a micro-tipped pipette attached to a gas bottle trap and a vacuum. The opening was closed usingJet self-curing acrylic paste obtained from a dental supply house. The entire procedure required that the fish be out of water no more than twenty-five minutes. Since Trichogaster trichopterus has the advantage of having a labyrinth organ, this presented no special problem.

Twenty-one fish were subjected to each treatment. Fish with each treatment were placed in dyadic encounter situations with fish of the same treatment and each of the other five treatments. Three replicates were made of each dyadic encounter for a total of sixty-three encounters.

After a recovery period of forty-eight hours, each isolated fish was placed in one of four large experimental tanks in which the agonistic encounters were to occur. These tanks were 30 x 46 x 180 centimeters and were constructed of marine plywood which was enameled white, and had glass fronts. By means of opaque dividers the tanks were divided into eight equal compartments in which the fish could still be maintained in isolation until the actual encounter. A period of twenty-four hours in which the fish were allowed to become accustomed to the experimental environment then followed.

To begin the bout, the dividers were removed between pairs of fish and their behaviors recorded until the encounter ended either in capitulation by one fish or, as occurred in three of the sixty-three fights, both of the fish stopped fighting and began to swim about the compartment in an exploratory fashion. Selected movements were recorded on an Esterline-Angus event recorder by two operators, one assigned to each fish.

Behavior Patterns

Motor patterns utilized were described for *T. trichopterus* in detail by Miller (1964) and are not redescribed below. The units measured in this study are as follows:

Latency to approach - The number of seconds from the moment the opaque divider was lifted free of the water between the two fish until one of the two fish swam toward the other fish to within two centimeters of the latter.

Latency to Lateral Display - The number of seconds from the lifting of the opaque divider between two adjacent fish until one fish fully erects its dorsal and ventral fins after having approached the second fish.

Number of Butts and Bites - The number of times a fish would either grasp the body of the other fish (biting) or would propel itself against the other fish making contact with the body of the other fish with the lips (butts). No attempt was made to differentiate between butts and bites.

Number of Tail Beats - The number of times one fish would thrust its tail and caudal peduncle toward its opponent while remaining stationary in the water by reverse beats of its pectoral fins.

Fight Duration - The period of time from the approach until one of the fish showed an appeasement posture or until both fish suddenly stopped fighting. (The latter occurred only three times in sixty-three fights).

Number of Opercle Spreads - The number of times a fish flared its gill covers giving an enlarged frontal view of the head. This was counted if the fish was seen to fold its dorsal fin, curve its body downward, droop its tail and remain in a stationary position facing its opponent; this movement is not as easily determined in *T. trichopterus* as in some other Anabantids (see Frey, 1970).

Number of Parallel Swims - The number of times both fish swam further than five centimeters in positions roughly parallel to one another.

Number of Air Intakes - Described by Wimmer (1970) as Dashes to the Surface, it is the number of times a fish makes a quick movement to the surface for the purpose of taking air into its labyrinth organ.

Tissue Study

Fish were sacrificed immediately after the fights and their brains were removed and fixed in neutral, buffered formalin in preparation for sectioning at ten microns, and staining with haematoxylin-eosin.

From slides of normal brains the major nuclei were distinguished, then those nuclei which were missing from the brains of the various ablated preparations were examined.

The major nuclei are briefly described below and are illustrated in Figures 3 to 11. A more detailed analysis was presented by Nieuwenhuys (1959).

Slides of normal fish were compared to slides of ablated fish. Drawing of operations one and two are not included, since those individuals were normal, nor are drawings of operation six, since the entire forebrain was removed. Figures 12 to 17 are representative of operations three, four, and five. Operation three involved removal of lateral areas of the forebrain, medial and posterior areas were removed in operation four, and operation five was a unilateral extirpation.

Bulbus olfactorius - sensory axons from the nasal mucosa enter the olfactory bulbs anteriorly, cover the surface of the bulb and terminate in the glomeruli olfactorii. These glomeruli are found in a layer just under the surface of the olfactory bulb. Proximal to the glomeruli are the large mitral cells whose dendrites terminate in the glomeruli.

Nucleus olfactorius anterior - found in the medio-dorsal area of the olfactory bulb. Nieuwenhuys (1959) as well as Holmgren (1920) observed the dendrites of these cells to terminate in widely separated glomeruli.

Nucleus nervi terminalis - situated between the olfactory bulb and the telencephalon. It consists of large cells set in a rosette which perform a neurosecretory function (Nieuwenhuys, 1960b). Fiber connections have not been reported with the terminalis nerve.

Area olfactoria medialis - has two major divisions.

Dorsal zone - near the sulcus limitans telencephali with parts near the anterior commissure. It lies in front of the pars precommissurealis superior, above the pars supracommissuralis and behind the pars postcommissuralis which merges with the pars intermedia. This acts as a transition zone between the area olfactoria medialis and the area olfactoria posterior.

Ventral zone - the pars precommissuralis inferior which merges into the pars commissuralis and grades into the nucleus preopticus.

Area olfactoria lateralis - large neurons situated more dorsally and immediately above the fissure endorhinalis.

Area olfactoria posterior - a posterior extension of the ventral zone of the area olfactoria medialis.

Area olfactoria dorsalis - has five major divisions.

Pars dorsalis - lies in the dorsal part of the area dorsalis and may be ill defined in some species. It is rather clear in the blue gourami.

Pars medialis - lies medial to the pars dorsalis on the dorsal part of the sulcus limitans telencephali.

Pars lateralis - terminates ventrally where the tela choroidea joins the brain. At the posterior end the transition zone is equivalent to Sheldon's nucleus pyriformis (as cited by Nieuwenhuys, 1960b) and lies between the pars lateralis of the dorsal area and the posterior olfactory area.

Pars magnocellularis - dorsomedial part of the dorsal area beneath the cell layer bordering the ventricle.

Nucleus preopticus - between the anterior commissure and the optic chiasma. The basal part extends laterally forming the recessus preopticus.

The general brain pattern of *T. trichopterus* is shown in Figure 2. Brain nuclei of *T. trichopterus* are outlined in Figures 3-11. As near as may be determined from the literature, this is the first attempt to comprehensively describe the forebrain nuclei of *T. trichopterus*.

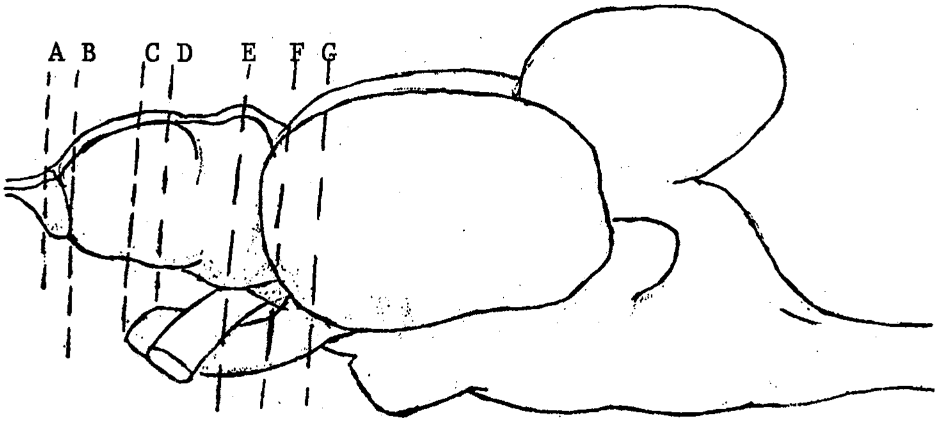

Figure 2. Brain of <u>Trichogaster trichopterus</u>, side-view.

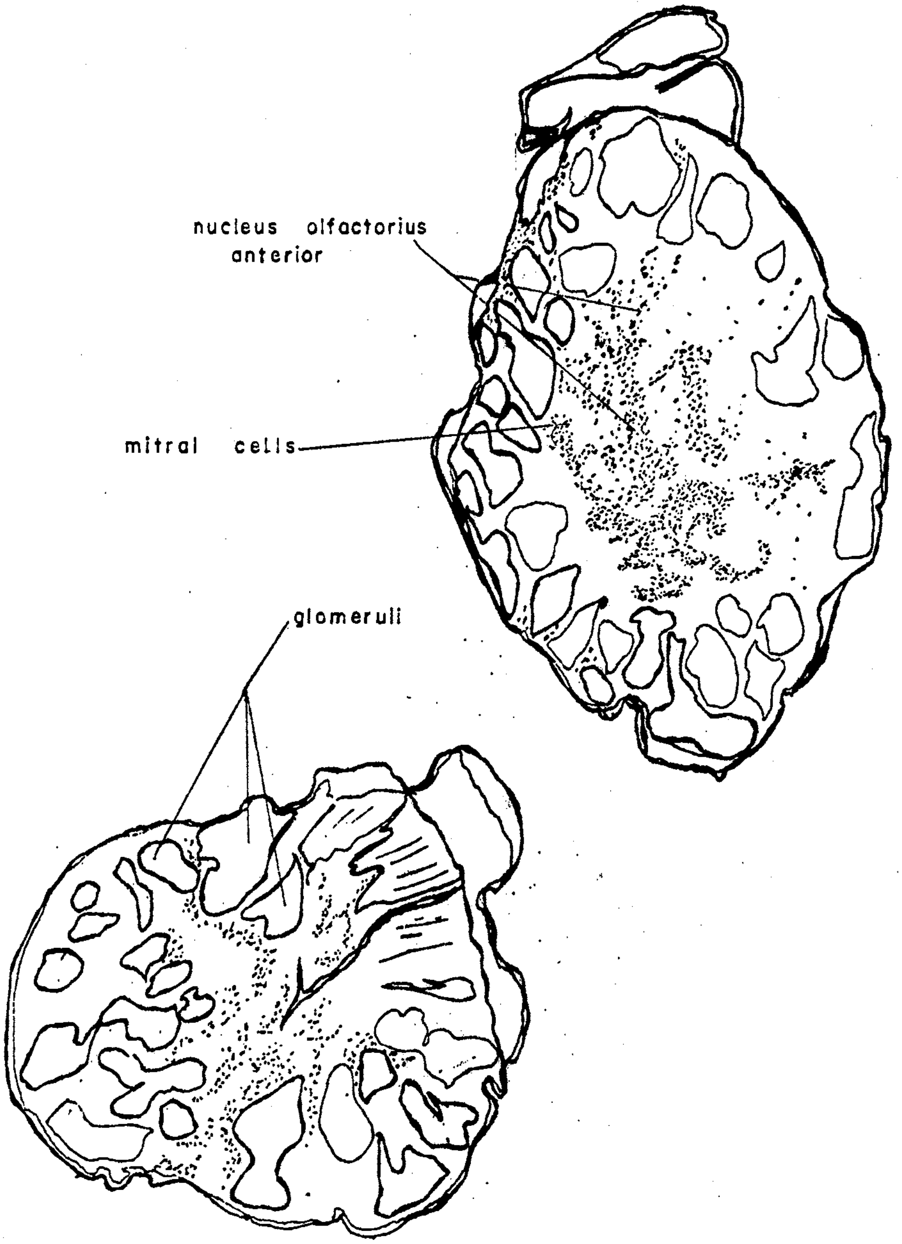

Figure 3. Cross section of blue gourami olfactory taken near line A on Figure 2.

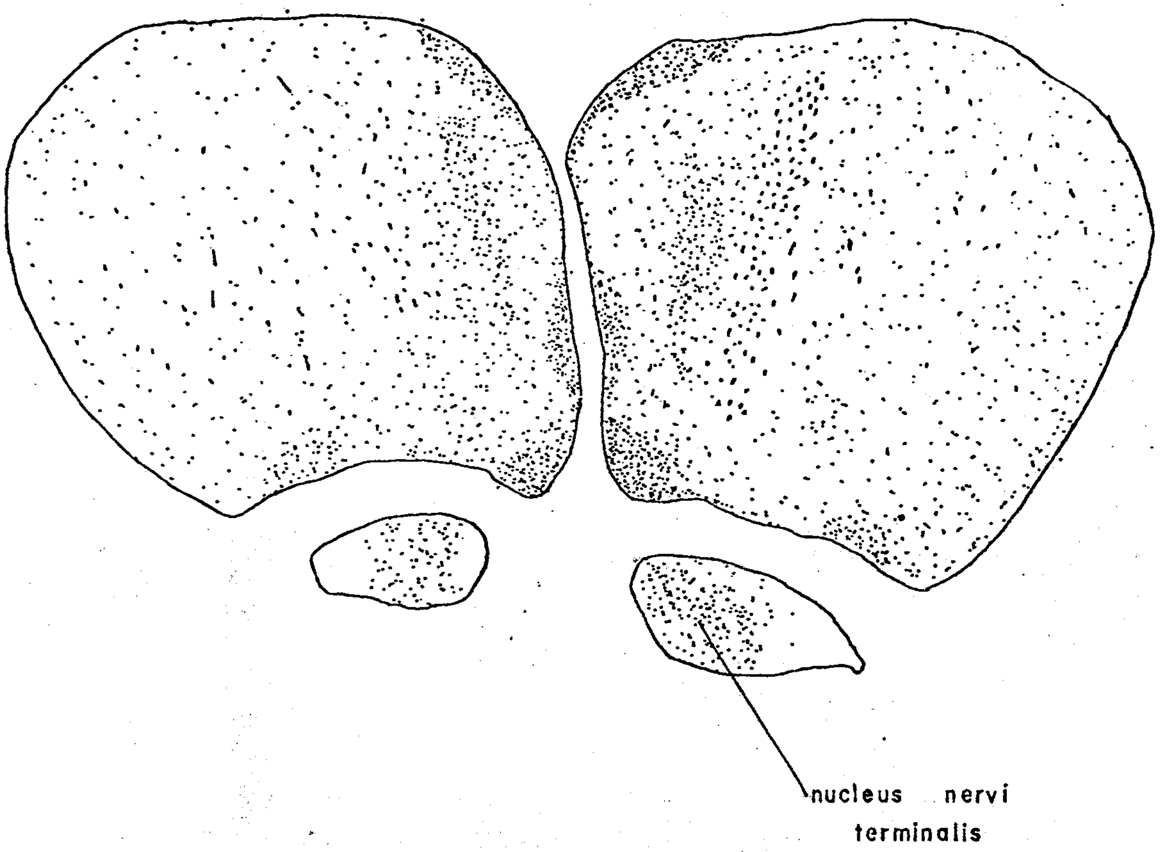

Figure 4. Cross section of the posterior portion of the olfactory bulbs and the anterior portion of the forebrain of the blue gourami taken at approximately level B of Figure 2.

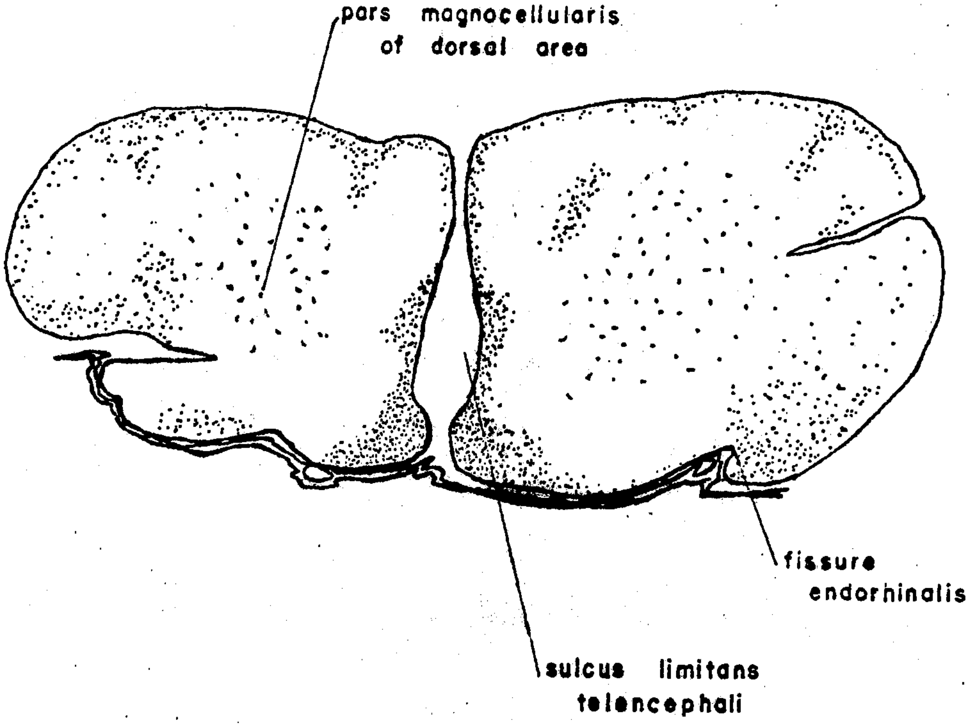

Figure 5. Cross section of the blue gourami forebrain taken at line C of Figure 2.

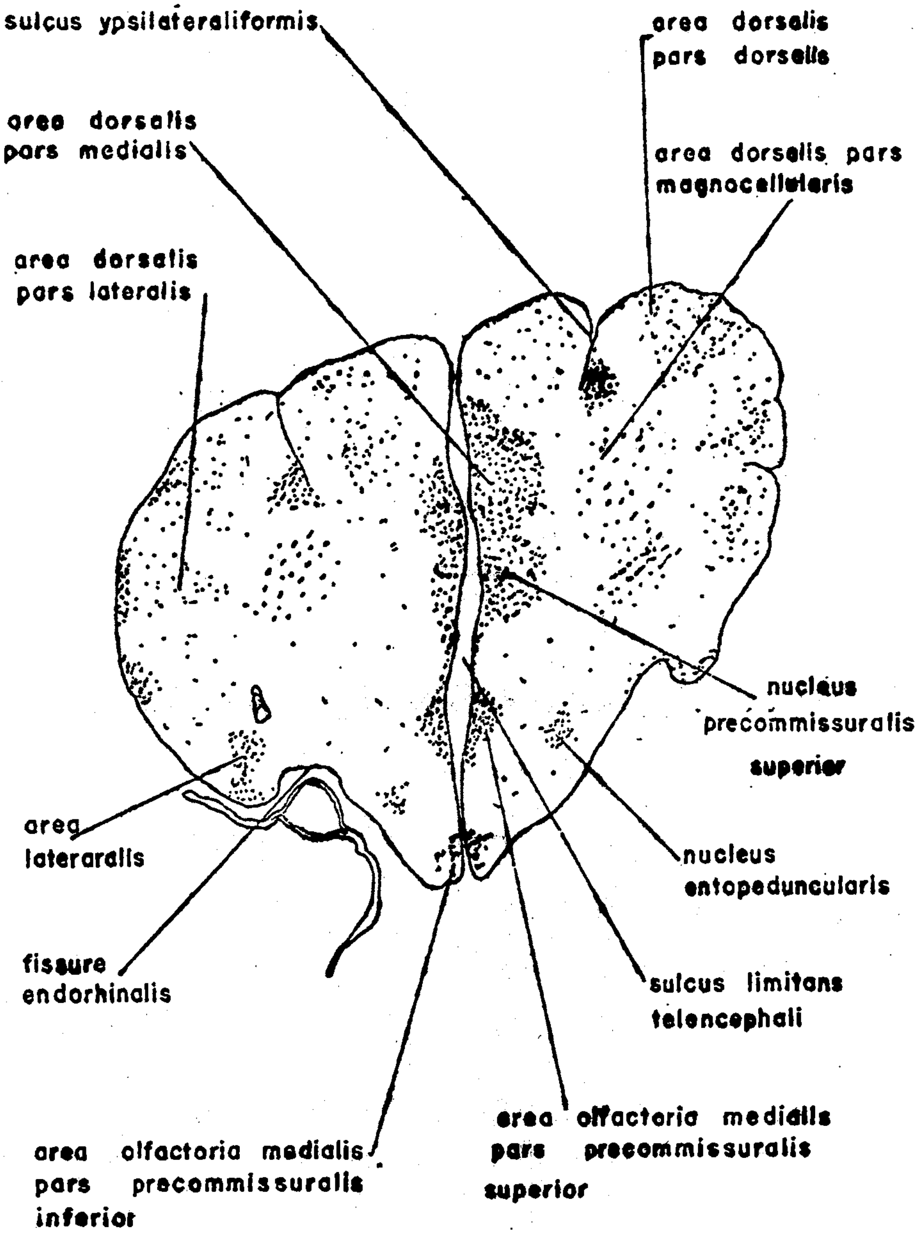

Figure 6. Cross section of the glue gourami forebrain taken at line D of Figure 2.

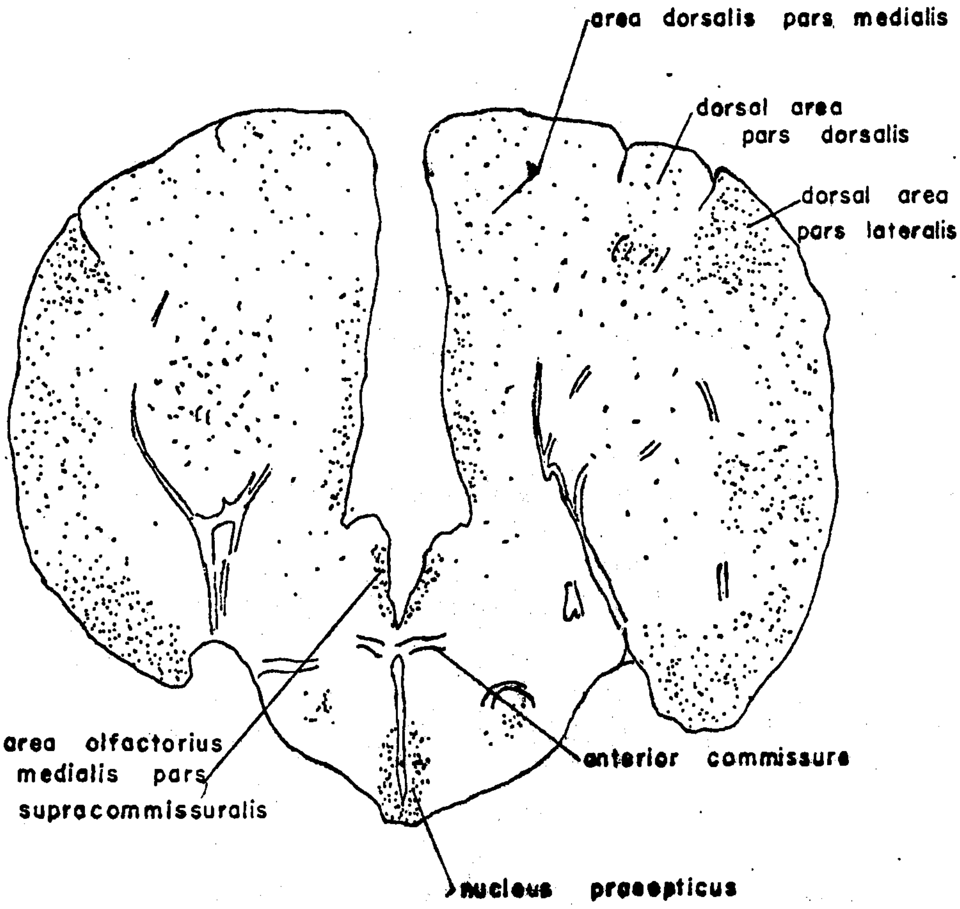

Figure 7. Cross section of the blue gourami forebrain taken at line E of Figure 2.

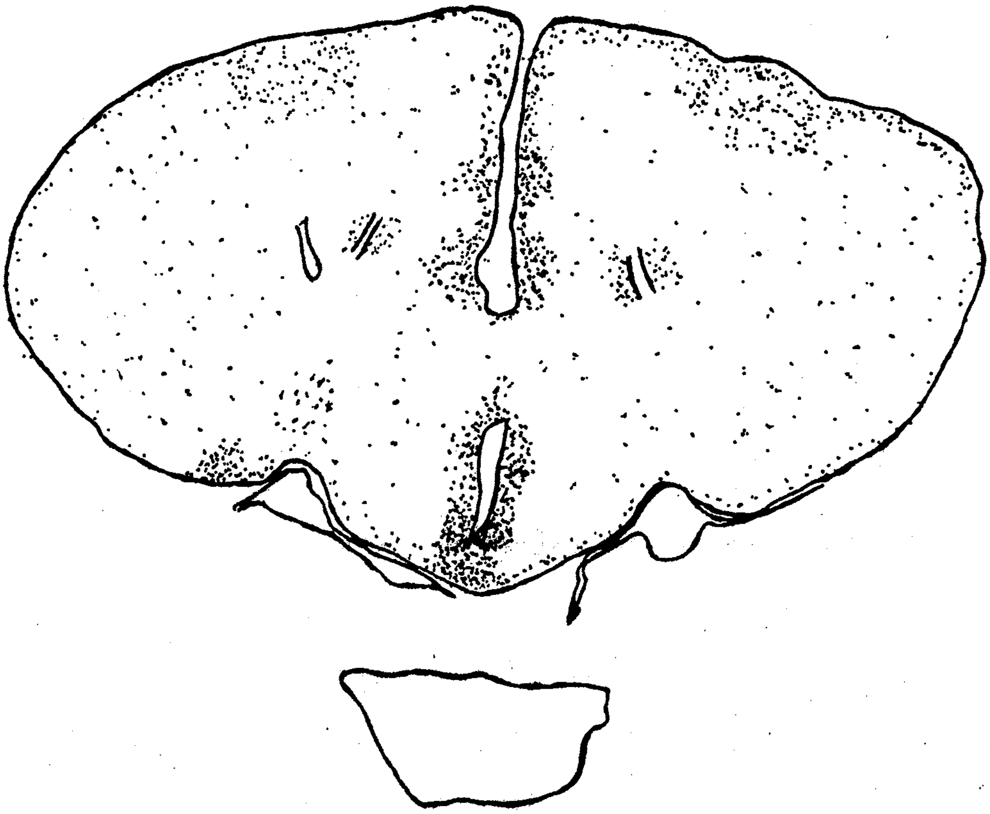

Figure 8. Cross section of the blue gourami forebrain taken from line E of Figure 2.

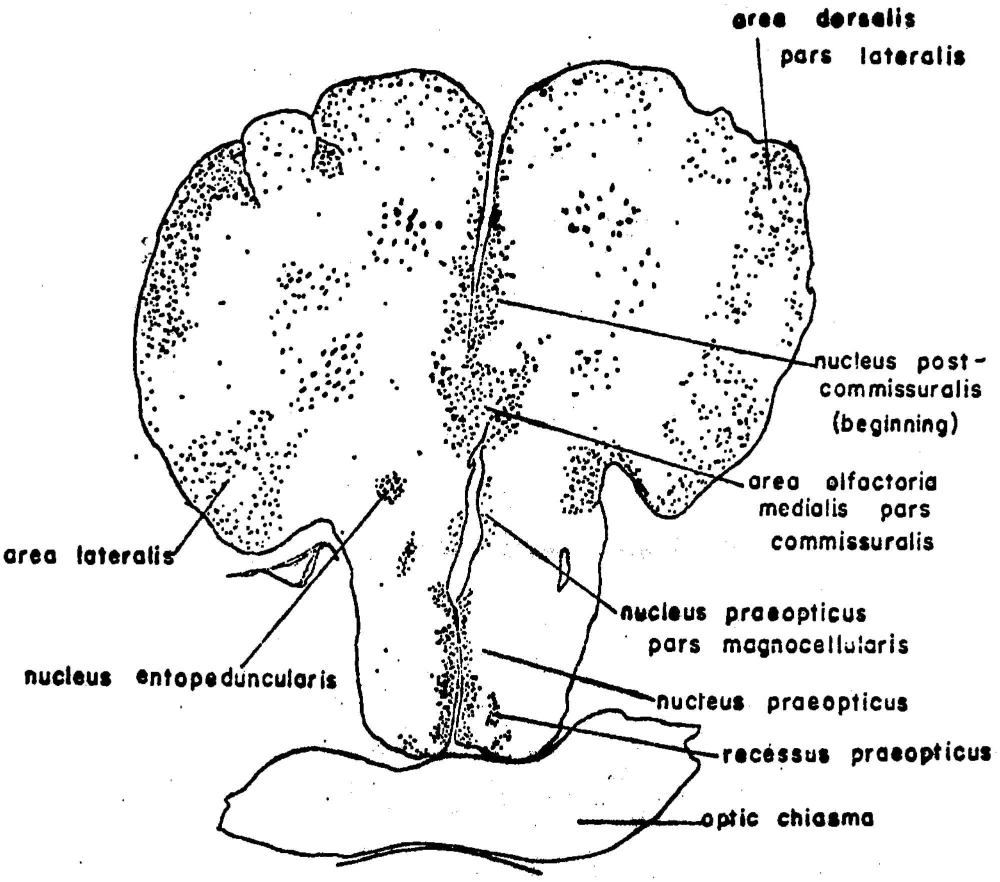

Figure 9. Cross section of the blue gourami forebrain taken at the level of line F of Figure 2.

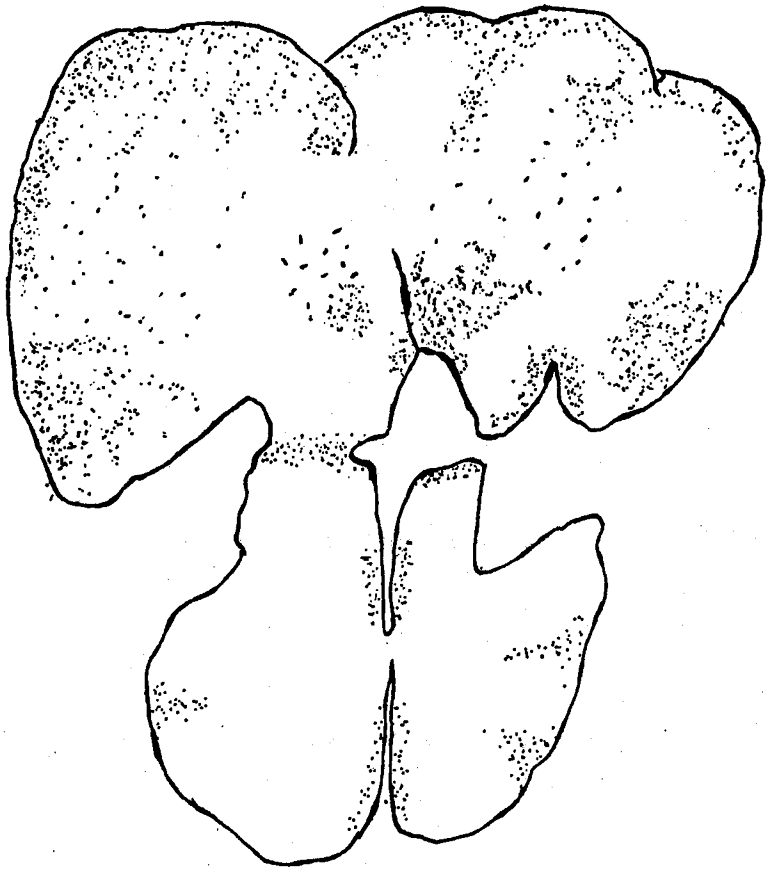

Figure 10. Cross section of the blue gourami forebrain and optic nerves taken at line G of Figure 2.

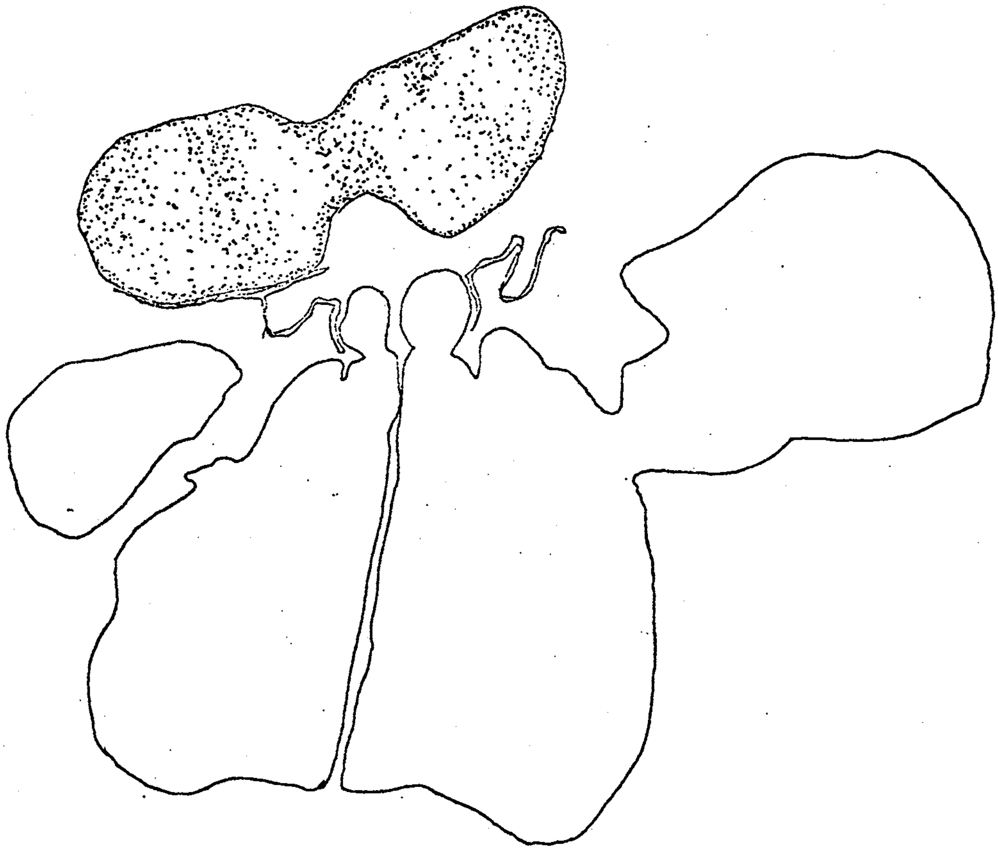

Figure 11. Cross section of the posterior of the blue gourami forebrain taken at line G of Figure 2.

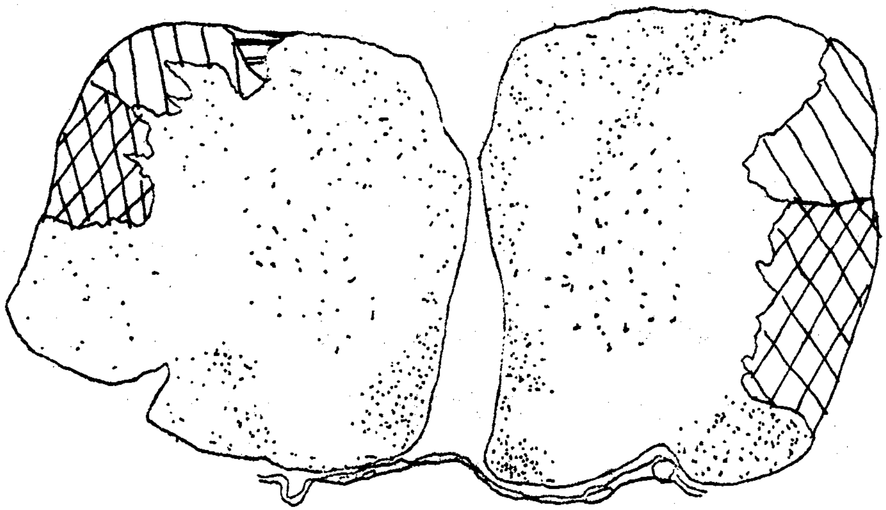

Figure 12. An example of operation three from the level of line D of Figure 2. Lateral lesions were made.

▧ pars dorsalis of the dorsal olfactory area removed.

▩ area lateralis removed.

▤ pars dorsalis of the dorsal olfactory area removed.

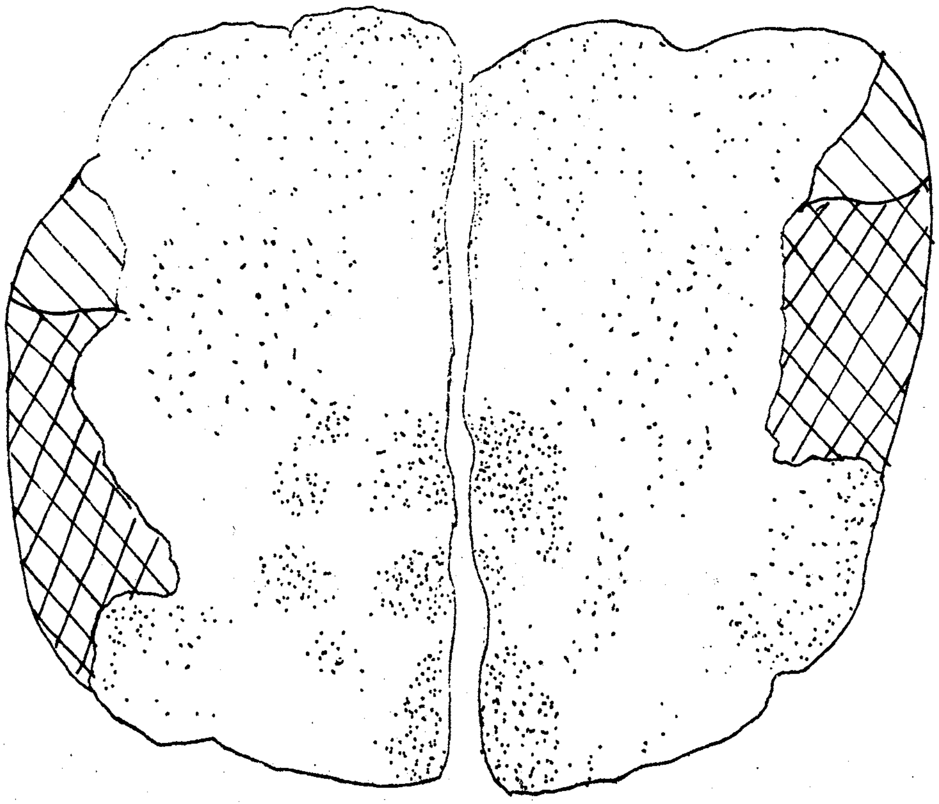

Figure 13. An example of operation three, which involved lateral ablations at the level of line D of Figure 2.

▧ pars lateralis of the dorsal olfactory area removed.

▦ area lateralis removed.

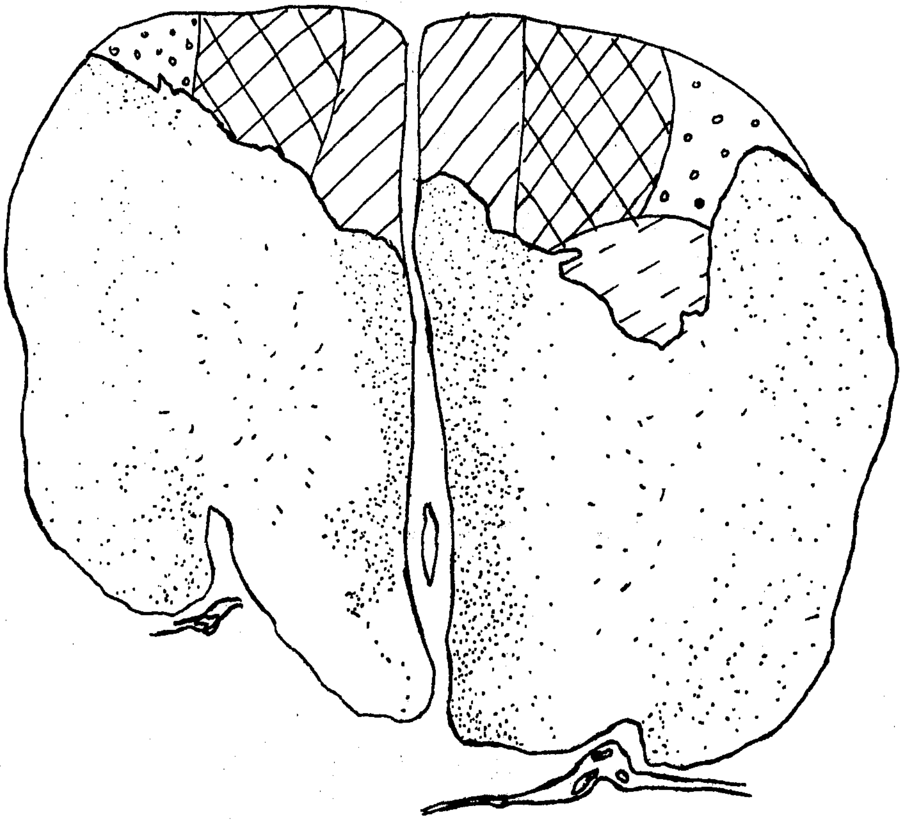

Figure 14. An example of operation four which involved medial and posterior ablations (from the level of line D of Figure 2).

▨ pars medialis of the dorsal olfactory area.

▩ pars dorsalis of the dorsal olfactory area.

⁘ pars lateralis of the dorsal olfactory area.

⁄ area olfactoria somatica.

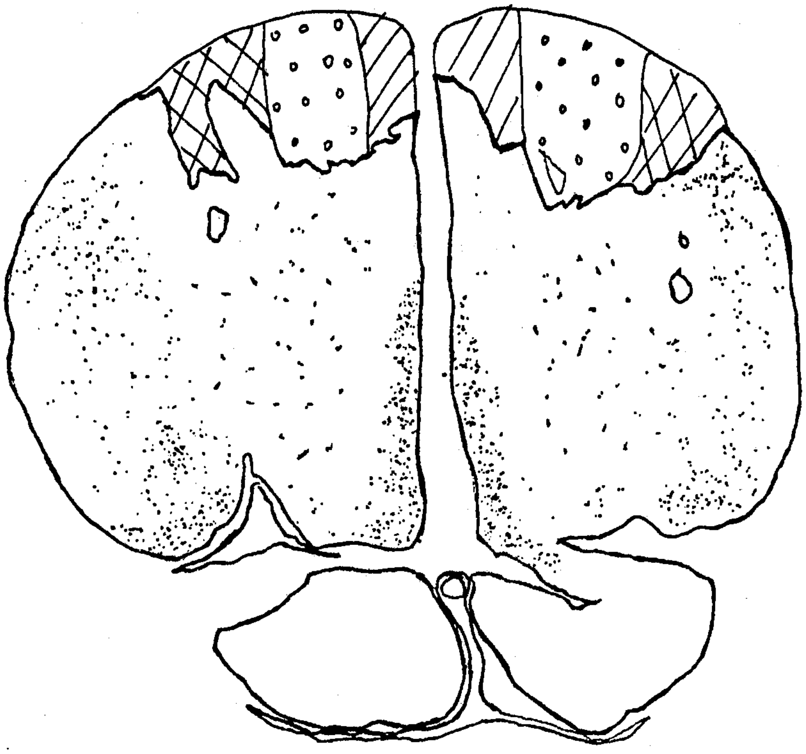

Figure 15. An example of operation four which involved medial and posterior ablations (from the level of line F of Figure 2).

▨ pars medialis of dorsal olfactory area.

⁘ pars dorsalis of dorsal olfactory area.

▩ pars lateralis of dorsal olfactory area.

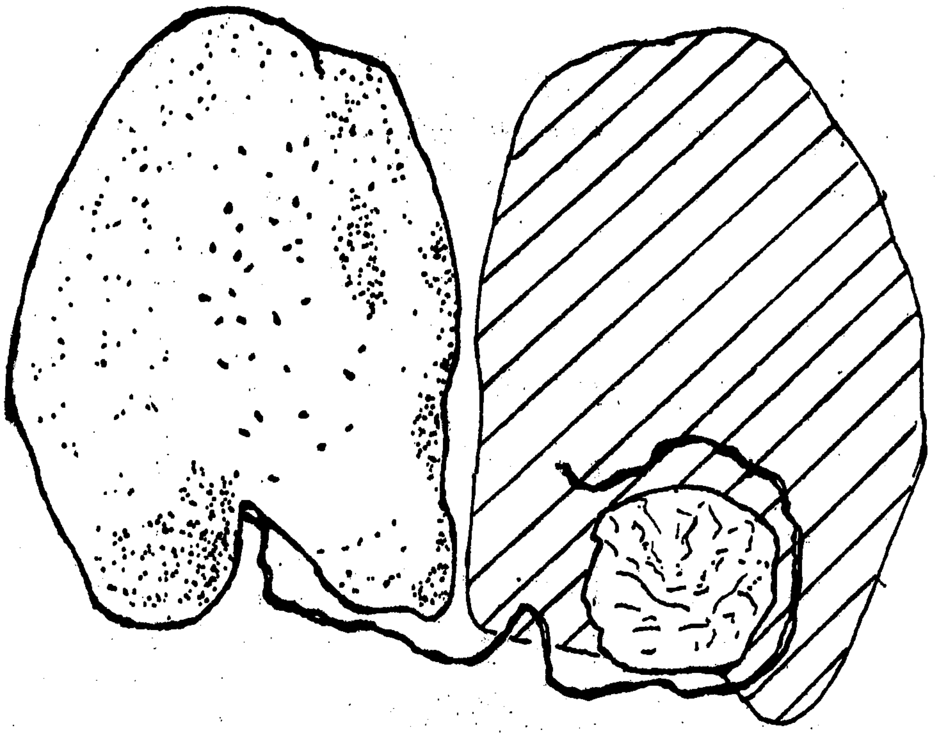

Figure 16. An example of operation five which involved unilateral ablation of the forebrain.

▨ ablated area.

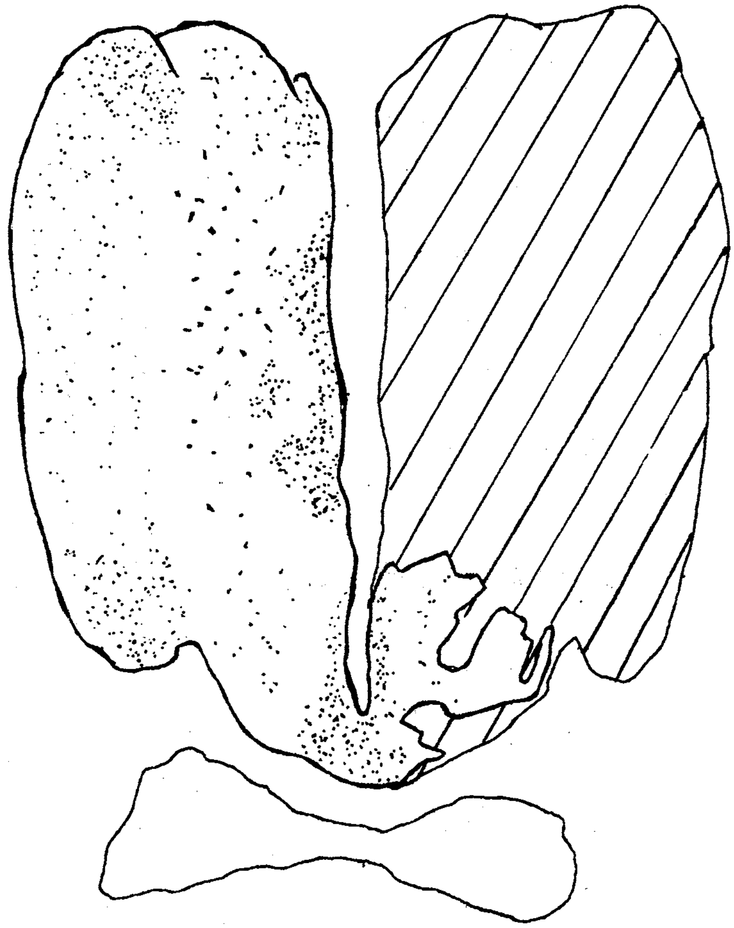

Figure 17. An example of operation five which involved unilateral ablation of the forebrain.

▨ ablated area.

CHAPTER III

OBSERVATIONS AND DISCUSSION

Multivariate analysis, testing each variable for differences among groups and for correlations with other variables, showed there was no interaction between effects of operation on observed fish and operation on competitor. If fact, the treatments to which the competitor was subjected appear not to effect the reactions of observed fish. The treatments produced significant differences in fight duration and the number of opercle spreads. There were significant correlations among the following variables: number of parallel swims, fight duration, number of air intakes, and number of opercle spreads. The correlations were, however, low; usually between .3 and .6.

Study was also made of the amount of overall activity. Sums of behavioral units for fish receiving each operation versus itself (three dyadic encounters summed) appear in Table I. There is a significant difference in the number of activities performed by fish which received operation six and the number of activities performed by fish which received other operations. Considerable difference also exists between the sums of fish receiving operations three and four and those receiving operations one, two, and five.

Activity sums for all fish of a given operation (eighteen dyadic encounters per operation type) are shown in Table II. The sum of behavioral units in column 10 of Table IIA excludes the highly variable behavioral units shown in Table IIB and may therefore be a more reliable index of comparison. While in most cases the sums of activity for operations three and four are low, they won fourteen and thirteen of their fights respectively, out of eighteen, while other operations remained near the halfway point.

TABLE I

SUMS OF BEHAVIOR ACTIVITIES PERFORMED BY FISH IN THREE DYADIC ENCOUNTERS, EACH TREATMENT VERSUS ITSELF ONLY

Operations	Butts & Bites	Fin tugs	Tail beats	Fight duration	Opercle spread	Air intakes	Parallel swims	Total units
1 vs. 1	235	35	34	3168	12	33	3	352
2 vs. 2	238	29	4	3744	28	34	32	365
3 vs. 3	83	11	19	3854	2	8	3	126
4 vs. 4	62	6	6	2956	2	5	9	90
5 vs. 5	344	26	93	6240	11	31	47	552
6 vs. 6	1	1	1	2048	0	7	0	10

Tables III and Iv show average activity sums of each treatment versus controls 1 and 2 respectively. Table V shows average activity sums of each treatment versus both controls 1 and 2.

Although a larger number of fish were used in this study than in the majority of earlier studies, it is not reasonable to make such concrete statements about forebrain function as did many of the earlier investigators, such as Hale (1956 a,b) or Noble (1936, 1937). A large variability was found within replicates. This may possibly be due to the species of fish chosen of the crude methods of forebrain extirpation, which produced several non-uniform ablations (see Figures 12 through 17).

TABLE II

TOTAL ACTIVITY SUMS PERFORMED BY FISH OF A GIVEN TREATMENT*

A.		Approach Latency		Latency to Lateral Display					
Operat.	Number of approaches	Time (sec)	Ave. time	Butts& Bites	Time (sec)	Fin tugs	Number of wins out of 18	Tail beats	Total behavior units
1	15	1538	103	553	2550	59	8	57	669
2	12	655	55	726	2034	114	8	72	912
3	13	1616	124	298	2698	51	14	38	387
4	9	1977	220	615	2771	49	13	120	784
5	12	1762	147	854	3708	87	9	120	1061
6	7	1668	238	116	3731	23	11	35	174

B. Operation	Fight duration	Opercle spread	Air intakes	Parallel swims	Total sum of behav. units
1	9592	42	90	42	753
2	11076	48	72	43	1003
3	10325	32	34	23	442
4	9353	11	44	30	825
5	16466	32	88	34	1127
6	9820	10	41	19	203

*All numbers on this table were rounded to the nearest whole number.

While it was not possible to find statistical significance in differences among behaviors which might reflect specific forebrain functions, a close perusal of Tables I through V indicates that there was, in fact, some type of fairly uniform change taking place due to the operations. Generally, there was less overt activity among fish that received operations three, four, and six (particularly the latter), than among fish that received operations one, two, and five.

TABLE III

AVERAGE ACTIVITY SUMS PERFORMED BY FISH IN DYADIC ENCOUNTERS BETWEEN EACH TREATMENT AND CONTROL TREATMENT 1

Operat.	Lat. to lateral display	Lat. to appr.	Butts and Bites	Fin tugs	Tail beats	Oper. spds.	Paral. swims	Air intakes	% of wins	Fight durat.
1	99.0	28.3	39.2	5.8	5.7	2.0	.5	5.5	50	528.0
2	115.3	99.3	3.0	3.0	3.0	1.3	.6	1.0	30	262.0
3	40.3	.6	5.6	1.0	.3	.6	.3	1.3	100	253.3
4	35.0	0.0	2.3	0.0	.3	.3	.3	1.0	100	373.3
5	158.6	148.0	72.6	13.3	1.6	2.6	2.0	6.3	30	936.6
6	173.6	14.6	2.6	1.0	0.0	0.0	0.0	1.0	60	309.3

Fish that received treatment two, the sham operation, showed a lowered latency to respond to stimuli. While in overall numbers of overt agonistic actions and in general post-operative behavior they did not differ grossly from normal fish, they were the quickest to approach their opponent and the quickest to lateral display except in bouts with normal fish. This indicates the possibility of some hyperreactivity or increased alertness due to operational shock.

TABLE IV

AVERAGE ACTIVITY SUMS PERFORMED BY FISH IN DYADIC ENCOUNTERS BETWEEN EACH TREATMENT AND CONTROL TREATMENT 2

Operat.	Lat. to lateral display	Lat. to appr.	Butts and Bites	Fin tugs	Tail beats	Oper. sprds.	Paral. swims	Air in-takes	% of wins	Fight durat.
1	211.0	9.3	9.6	.6	1.3	1.3	1.0	1.0	60	262.0
2	163.0	12.8	30.6	4.8	.7	4.2	5.3	5.6	50	624.0
3	159.0	27.0	.6	6.0	1.3	.3	.6	2.0	100	441.3
4	70.0	32.7	109.6	2.7	6.0	.6	3.0	4.0	30	322.7
5	38.0	90.0	26.3	4.7	5.3	2.0	.6	5.0	30	562.7
6	90.7	0.0	18.6	2.6	3.0	2.0	.6	3.3	60	748.7

TABLE V

AVERAGE SUMS OF ACTIVITY FOR FISH OF EACH TREATMENT VERSUS CONTROL TREATMENTS 1 AND 2

Operat.	Lat. to lateral display	Lat. to appr.	Butts and Bites	Fin tugs	Tail beats	Oper. sprds.	Paral. swims	Air in-takes	% of wins	Fight durat.
1	155.0	18.5	24.4	3.2	3.5	1.65	1.8	3.3	55	395
2	139.2	56.1	21.3	3.9	1.9	2.75	3.0	3.3	40	443
3	99.7	13.8	3.1	3.5	.8	.50	.5	1.7	100	347
4	52.5	16.4	55.9	1.3	3.4	.50	.5	2.5	65	348
5	98.3	119.0	49.5	9.0	3.5	2.30	1.3	5.7	33	750
6	132.2	7.3	10.6	1.8	1.0	1.00	.3	2.2	60	529

Fish which received lateral lesions, treatment three, which Noble (1936) found to cause a lack of coordination in breeding and care of young in Cichlids, appeared slightly more active than normal in exploratory behavior preliminary to the agonistic bout. They showed a very low number of fin tugs, which Frey (1970) found to be highly correlated with winning or losing the bout, yet they won fourteen of their eighteen bouts and in this respect were superior to all other operations. They won all of their bouts against normals and sham operants despite the fact that they were less active overall. This suggests they may have used more force when they did react (Hosch, 1936). It may then be postulated that this operation involved the removal of some type of inhibitory center which regulated the intensity of the aggressive behaviors in the fish. Opponents of these fish, although they were well-bruised, did not appear particularly more bruised than the opponents of normals, but their fins were generally badly shredded. Since fight durations are generally brief, gross differences in tissue damage resulting from fights could not be expected.

Fish which received treatment four (medial and posterior lesions, particularly in the area thought to be the primordium hippocampi from which Hale (1956a) reported marked changes in aggressive behavior) showed a similar number of aggressive behaviors and wins. Fish with this operation did not readily approach normals or shams and their overall average approach time (Table II) was second only to fish who received operation six. This indicates an increase in latency to respond. Therefore, the same hypothesis as for fish receiving operation three might apply to those receiving operation four. This type of evidence appears to coincide with Aronson's (1963, 1971) hypothesis that the forebrain is a general arousal area.

Fish receiving treatment five appeared much like normals. In general the numbers of agonistic behaviors performed by these fish were slightly higher than those of the normals but were usually fairly close to the normal numbers. The loss of one half of the forebrain may therefore be compensated for by the other half. Fish with this operation would have all basic forebrain areas present, but would have only half as much as normal fish. Thus, they may be able to function normally.

Fish which received treatment six showed the most dramatic behavioral change with significantly lower numbers of agonistic behaviors and long reaction latencies. In this group the fish were slow to react to one another and fights between operants were sluggish. This again coincides with the findings of many earlier investigators who postulated the forebrain to be an arousal center. Post-operatively for a period of several hours these fish showed bazarre behavior indicating an inability to coordinate and properly orient themselves in the water. Two were seen to swim on their tails, three on their heads in a bobbing fashion, and two continually swam into a corner of their isolation bucket repeatedly bumping their heads on the sides of the buckets. These aberrant behaviors ceased within four hours of the operations. This suggests that the forebrain may well control more than the olfactory sense and arousal.

These data, although generally not statistically significant for the reasons cited above, or perhaps simply because of the small sample size, seem to support Aronson's hypothesis. The high variability in responses found in this study indicates that much more discrete areas should be extirpated in fairly large number of fish in order to truly test Aronson's hypothesis.

CHAPTER IV

SUMMARY

1. Forebrain ablations of four varying degrees of severity with two types of controls were performed on one hundred twenty-six male blue gouramis. Animals were then placed in dyadic, agonistic encounter situations and quantitative data recorded by observers on an event recorder.

2. Serial sections of the brains were then made and experimental animals compared with controls to determine the extent of forebrain damage.

3. The major brain nuclei were mapped out from line drawings of intact specimens. These drawings were compared to drawings of lesioned brains to determine the missing nuclei.

4. Little statistical significance was found among differences in behavior patterns in specimens subjected to the various operations. However, positive correlations were found among the frequencies of the agonistic activities measured within any group with similar lesions. Summed data of agonistic behaviors showed considerable differences among treatment groups.

5. Fish who received operations three and four, partial ablations showed reduced numbers of behavioral units but usually won their dominance bouts.

6. Fish who received operation five, a unilateral extirpation

appeared nearly normal.

7. Fish who received operation six, a complete bilateral extirpation of the forebrain, showed bazarre behaviors and a lack of responsiveness.

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APPENDIX A

FOREBRAIN NUCLEI NOMENCLATURE FROM ARIENS KAPPERS _ET_. _AL_. (1936)

ARIENS KAPPERS	SHELDON	HOLMGREN	JOHNSON	HERRICK	HALE (1956)
A. OLFACTORY BULB					A. OLFACTORY BULB
VENTRICULUS BULBUS OLFACTORII					
NERVOUS TERMINALS		CAUDAL CELL GROUP OF THE BULB			
NUCLEUS OLFACTORIES ANTERIOR PARS BULBARIS	NUCLEUS OLFACTORIUS ANTERIOR	NUCLEUS OLFACTORIUS ANTERIOR			NUCLEUS OLFACTORIUS ANTERIOR PARS BULBARIS
NUCLEUS OLFACTORIES ANTERIOR					
B. MEDIAL OLFACTORY AREA					B. MEDIAL OLFACTORY AREA
EPISTRIATUM			NUCLEUS OLFACTORIUS MEDIALIS		
	CORPUS PRECOMMISSURALIS		PRECOMMISSURALE		PRECOMMISSURALE
			NUCLEUS OLFACTORIUS ANTERIOR PARS PRECOMMISSURALIS		NUCLEUS OLFACTORIS ANTERIOR
			NUCLEUS PRECOMMISSURALIS SUPERIOR		NUCLEUS PRECOMMISSURALIS SUPERIOR
NUCLEUS SUPRACOMMISSURALIS		LATERAL OLFACTORY NUCLEUS	NUCLEUS PRECOMMISSURALIS INFERIOR		NUCLEUS PRECOMMISSURALIS INFERIOR
					NUCLEUS SUPRACOMMISSURALIS
					C. POST COMMISSURAL
		NUCLEUS POSTCOMMISSURALIS			NUCLEUS POSTCOMMISSURALIS
D. PREOPTIC PORTION OF MEDIAL OLFACTORY AREA					D. PREOPTIC AREA
NUCLEUS PREOPTICUS PARVOCELLULARIS					NUCLEUS PREOPTICUS PARVOCELLULARIS
NUCLEUS PREOPTICUS MAGNOCELLULARIS					NUCLEUS PREOPTICUS MAGNOCELLULARIS
E. DORSAL OLFACTORY AREA				E. OLFACTOSOMATIC AREA	E. DORSAL OLFACTORY AREA
EPISTRIATUM LINGUA LATERALIS LINGUA MEDIALIS	NUCLEUS OLFACTORIUS DORSALIS	PARS STRIATALIS -	PRIMORDIUM HIPPOCAMPI	DORSOMEDIALIS OR PARS MEDIALIS	PARS MEDIALIS
		PRIMORDIUM PALLII			
		PRIMORDIUM PALLII PARS MEDIALIS			
AREA OLFACTORIAL LATERALIS	NUCLEUS OLFACTORIUS LATERALIS	PRIMORDIUM PALLII PARS DORSOLATEPALIS LATER THE GENERAL PALLIUM		PARS DORSALIS OR PARS DORSOLATERALIS	PARS DORSALIS
	PALEOSTRIATUM	PRIMORDIUM PALLII		OLFACTOSOMATICS	
		PARS LATERALIS		PARS LATERALIS NUCLEUS OCCIPITOBASALIS	PARS LATEPALIS
NUCLEUS TAENIA & POSSIBLY PART OF AREA OLFACTORIA LATERALIS & PART OF PALLIOPALLIUM	NUCLEUS TAENIE LOBUS PYRIFORIS	(A PRIMORDIUM HIPPOCAMPI)			
TUBERCULUM TAENIE					
F. LATERAL OLFACTORY AREA AREA			F. LATERAL OLFACTORY AREA	F. LATERAL OLFACTORY AREA	F. LATERAL OLFACTORY AREA
LATERAL OLFACTORY NUCLEUS	NUCLEUS COMMISSURALIS LATERALIS	NUCLEUS OLFACTORIUS LATERALIS			
G. AREA SOMATICA		G. AREA SOMATICA	G. SOMATIC PROJECTION TRACT		G. OLFACTO-SOMATIC AREA
THALAMO CORTIOALIS	NUCLEUS ENTOPEDICULARIS				SOMATIC AREA

APPENDIX B

COMPARISON OF FOREBRAIN NUCLEI NOMENCLATURE USED BY CONTEMPORARY INVESTIGATORS

Nieuwenhuys (1960)	Aronson (1968)	Hale (1956)	Droogleever Fortuyn (1961)	Schnitzlein (1966)
A. Olfactory bulb	A. Olfactory bulb	A. Olfactory bulb	A. Basal region	A. Olfactory bulb
		Nucleus olfactorius ant. pars bulbaris	Rostral continuation of P. hippo, anterior nucleus (bulbur part)	Nucleus olfactoris
B. Ventral area (subpallium)				
C/D/E. Dorsal part	C. Medial olfactory area	C. Medial olfactory area		
		Precommissuralis		
		C/D. Nucleus olfactorius ant.	C/D. Lateral septal nucleus ant. in septal region	C/D. Nucleus olfactorius ant.
			Olfactory nucleus (lobar part) in septal region	
		C/E. Nucleus precommissuralis superior	C/E. Median septal nucleus in septal region	C/E. Septal nuclei
			Nucleus of the diagonal band	
F/G/H. Lateral part		F. Nucleus precommissuralis inferior	F. Polymorph layer of basal olfactory tubercle	F. Septo-hippocampi nucleus lateral septal nucleus
			Bed nucleus of anterior commissuralis	
		Nucleus supercommissuralis		
		F/G. Post commissural	F/G. Post commissural	
		Nucleus postcommissuralis		
		F/H. Preoptic area	F/H. Preoptic area	F/H. Preoptic area
		Nucleus preopticus cellularis	Parvocellular preoptic nucleus	Nucleus preopticus
		Nucleus preopticus magno-cellularis	Magno-cellular preoptic nucleus	
		Nucleus preopticus parvo-cellularis recessi		Recessus preopticus
I. Dorsal area (pallium)	I. Dorsal olfactory area	I. Dorsal olfactory area		
Medial part	Pars medialis	Pars medialis	Primordium hippocampi	Primordial hippocampal formation
Central medial part (area somatica)			Medial region	
Dorsal part	Pars dorsalis	Pars dorsalis	Dorsal area	Primordial general pallium
Central dorsal part (area somatica)				
Lateral part A. Intermediate part B. Lateral part C. Medial part	Pars lateralis	Pars lateralis	Prepiriform area Considered in Basal area	Piriform area Primordium amygdale corticomedialis Primordium piriformalis pars ventralis Primordium piriformalis pars dorsalis
	Lateral olfactory area	Lateral olfactory area	Piriform lobe Dorsolateral nuclei Ventromedial nuclei	Piriform area
			Precommissuralis	
			Amygdala	
			Postcommissuralis	
	J. Olfacto-somatic area	J. Olfacto-somatic area		
	Nucleus entopeduncularis		Striate body	Striatum
			Nucleus entopediuncularis	Nucleus of the diagonal band

2

VITA

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Master of Science

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