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The Optomotor Response of a Forebrainless Fish, *Tilapia mossambica*

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INTRODUCTION

The present report deals with experiments in which the optomotor response of *Tilapia mossambica*, a cichlid fish that shows schooling behavior, was tested before and after forebrain ablation.

The function of the forebrain in fishes has been extensively reviewed by Aronson and Kaplan (1968) and Kaplan and Aronson (1969). They pointed out that removal of the forebrain affects a number of behaviors, including schooling. They cited several researchers (Noble, 1936; Hosch, 1936; Berwein, 1941), who upon ablating the fish forebrain found such alterations in schooling fishes as the inability to change direction, sluggishness, and a tendency to avoid other fish. Schooling, however, was not eliminated. In the present studies, the optomotor response was employed because of the difficulty in measuring schooling patterns directly (Cullen, Shaw and Baldwin, 1965; Hunter, 1966). Shaw and Tucker (1965) pointed out that when a fish is exposed to the classical optomotor stimulus (moving, vertical, alternating black and white stripes), several features of schooling are simulated. A classical response is seen when a fish swims in the same direction and at the same speed as the moving stripes. In a polarized school, a fish also swims at the same speed and in the same

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direction as its school members (Shaw, 1970). Two features of the optomotor response lend themselves to quantitative evaluation, namely, measurement of fish speed or r.p.m., and the ability of the fish to reverse swimming direction.

MATERIALS AND METHODS

OPTOMOTOR APPARATUS: The apparatus consisted of a stationary circular aquarium, 14 cm. in diameter by 15 cm. high, and a rotatable drum, 20 cm. in diameter by 20 cm. high (fig. 1). The inner surface of the drum was lined with alternating vertical black and white stripes, each stripe 0.6 cm. wide. Both the drum and the aquarium were filled with conditioned aquarium water. The drum was rotated at approximately 20 r.p.m.

THE FISH: Sixty-five juvenile and young adult *Tilapia mossambica* (Peters), 5 to 8 cm. standard length, from a stock kept at the American Museum of Natural History, provided the subjects. They were fed a balanced diet of fresh and dried food three times a week. The fish were housed in 15-gallon tanks divided by transparent glass plates into three equivalent compartments. One fish was kept in each compartment for at least one week before it was either given its initial test or operated on.

Forebrain ablations were carried out first by anesthetizing the fish in a 2 per cent urethane solution. Then a T-shaped slit was made in the skin just behind the eyes, the skin lifted back, and the connecting muscles below removed with an iridectomy scissors. A tiny hole was made in the bony skull and enlarged to about 0.7 square cm. by chipping of the bone.

The forebrain was ablated with a low-pressure aspirator. The sham operation was identical in procedure except that the forebrain was not removed. After testing, the brains were fixed in formalin and inspected to ascertain the removal of the forebrain.

THE GROUPS OF FISH AND THE TEST SCHEDULES: (1) Group 1 consisted of 25 fish, 15 forebrain ablates and 10 sham operates. The forebrain was ablated 60 days prior to the first test. Subsequent tests were five, 10, and 55 days after the initial test.

(2) Group 2 consisted of 20 fish divided into units of 10 fish each, forebrain ablates and sham operate control fish. They received three preoperative and four postoperative tests. The operation was performed five days after the third preoperative test, and the first postoperative test was made five days after the operation. The tests were five days apart, except for the last, the fourth postoperative test, which was carried out 45 days after the third postoperative test.

Groups 1 and 2 were tested during the winter and spring.

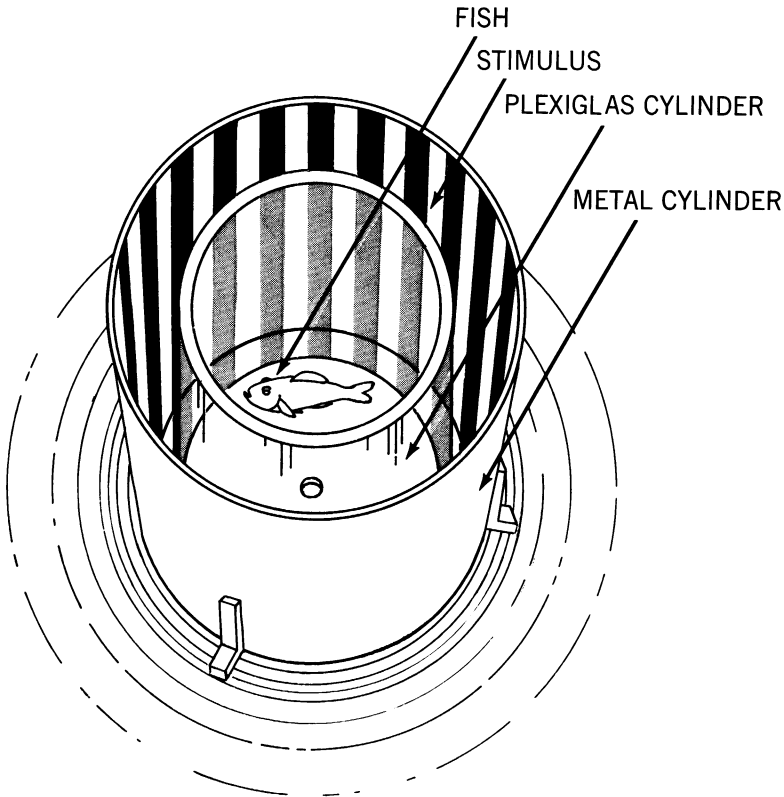


FIG. 1. Diagram of the optomotor apparatus.

(3) Group 3 was tested during the summer. This group contained 20 fish divided into two sets of 10 fish each. The major difference from the other two groups was that among the operated fish, initially, only the right lobe of the forebrain was removed. After the three postoperative tests in the hemi-forebrainless condition, the other lobe of five of the 10 hemi-forebrainless fish were ablated. The other five hemi-forebrain ablates and the sham operates underwent the regular "operation" procedure. Group 3 fish were tested nine times at five-day intervals.

Throughout the experiment, fish were invariably tested at the same time of day as in the initial test.

THE TEST: Each fish was carried by hand net from its individual chamber in the greenhouse to the laboratory, then placed into a 1-gallon tank for 10 minutes, permitting it some time to adjust to laboratory

conditions. Temperatures were approximately the same, 23 to 26° C. After this the fish was transferred by hand net to the circular aquarium of the optomotor apparatus.

At the end of another 10-minute adjustment period, the drum was started in whatever direction, clockwise or counter-clockwise, the fish happened to be heading. As the drum revolved, at about 20 r.p.m., the fish had to swim about 64 cm. per minute to maintain a speed constant with the drum. The drum r.p.m. and the r.p.m. of the fish were counted. At the end of each minute, drum direction was reversed giving 10 reversals during an 11-minute test.

RESULTS

In general, the results showed that sham operates swam in the same direction as the moving, alternating vertical black and white stripes, reversed their direction when the direction of stripe movement was reversed and tended to maintain an r.p.m. similar to the r.p.m. of the drum. Among the forebrain ablates, however, these behaviors were significantly modified.

REVOLUTIONS PER MINUTE: The revolutions per minute described by the fish of Groups 1 to 3 in relation to the drum r.p.m. are presented in figures 2-4. The r.p.m. of the fish is presented as a plus or minus, depending on whether fish swam faster or slower than drum speed. If they swam at drum speed, their r.p.m. is indicated as 0.

The means and standard deviations for Group 1 are presented in table 1. Significant differences were found when forebrainless fish were compared to the sham operates. The results are graphed in figure 2.

Results of Group 2 tests are graphically presented in figure 3. Means and standard deviations are listed in table 2 and significant differences are indicated. In table 2, it is clearly seen that there were no significant differences in the experimental categories prior to the ablation. After ablation, forebrainless fish swam significantly fewer r.p.m. Two months later, their r.p.m. had increased but not enough to eliminate the significant differences.

Results of Group 3 tests are summarized in table 3 and graphically presented in figure 4. Prior to the first operation, the r.p.m. of the two groups was not significantly different. The trend was toward an increase in r.p.m. However, among the sham operates, the r.p.m. during the third test was significantly greater than the r.p.m. during the first test. After the operation, when one lobe was removed, hemi-forebrainless fish swam significantly fewer r.p.m. than the sham operates. At day 25, the other lobe of the forebrain was removed from five of the ten hemi-forebrain

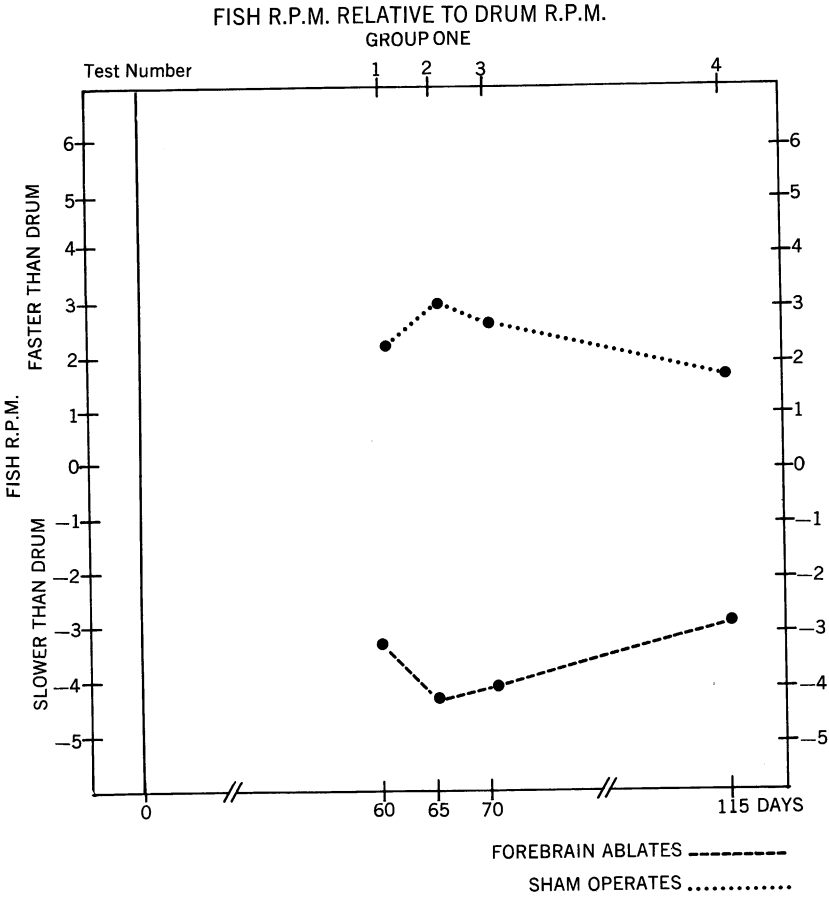


FIG. 2. Group 1. Graph showing r.p.m. of fish relative to drum r.p.m. If fish r.p.m. is greater than that of drum it is indicated as a plus, lesser than the drum, a minus. Vertical line at 0 days indicates day of ablation.

ablates. The totally forebrainless fish swam significantly fewer r.p.m. than the hemi-forebrain ablates and sham operates.

In addition, the r.p.m. during the third test among the sham operates was significantly greater than the r.p.m. during the eighth and ninth tests. Such a preoperative upward trend and postoperative downward trend was not seen among Group 2 fish where r.p.m. of the sham operates tended to remain the same throughout.

CORRECT REVERSALS: At the end of each minute, drum direction was

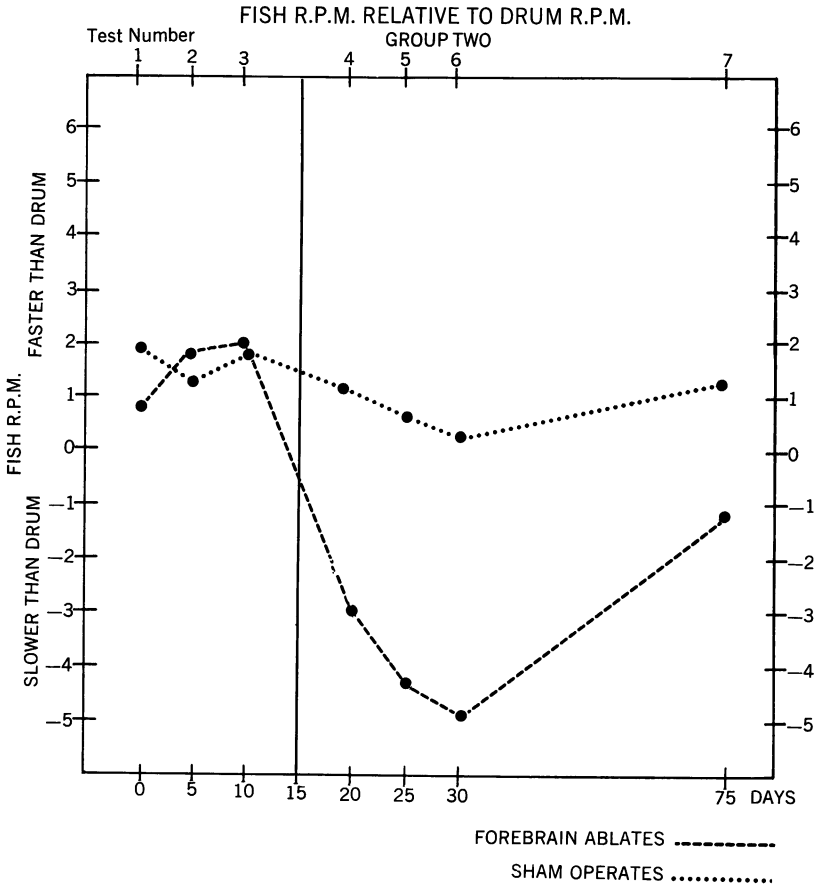


FIG. 3. Group 2. Graph showing r.p.m. of fish relative to drum r.p.m. If fish r.p.m. is greater than that of drum it is indicated as a plus, lesser than the drum, a minus. Vertical line at 15 days indicates day of ablation.

reversed and immediately accelerated to top speed. In order to respond to the drum reversal, the fish also had to change direction at the end of the minute. However, the fish did not always do so. Sometimes, if the fish and the drum were moving counter-clockwise and the drum reversed direction, the fish continued swimming counter-clockwise. When the drum again reversed to counter-clockwise, the fish was already properly oriented. This could not be considered either a correct or incorrect reversal. Thus, if a fish turned the first eight times in response to drum reversal but not on the ninth reversal, it did not have an opportunity

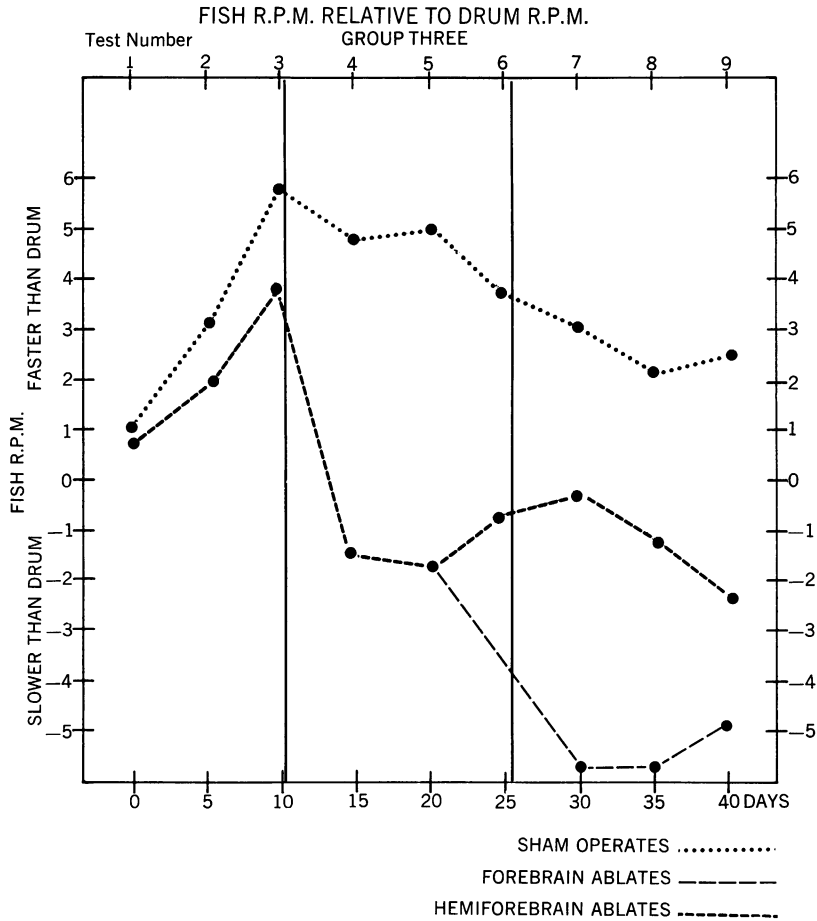


FIG. 4. Group 3. Graph showing r.p.m. of fish relative to drum r.p.m. If fish r.p.m. is greater than that of drum it is indicated as a plus, lesser than the drum, a minus. Vertical line after 10 days indicates day when half the forebrain was removed, and line after 25 days indicates day when remaining half of forebrain was removed from five of the 10 fish.

to make the tenth or last reversal. The score, therefore, was based on the fish turning eight out of nine times with a percentage score of 89.

Forebrainless fish did not reverse as often as did sham operates. The results of Group 1 are presented in figure 5 and table 4. Among Group 2 fish, in contrast to their preoperative activity, there was a significant decrease in reversals after the fish forebrain was ablated and the data

are presented in table 5 and figure 6. Among Group 3 fish, hemi-fore-brainless fish showed an initial drop in reversals, not significantly different, and in the remaining tests their reversal percentages were high.

TABLE 1
FISH R.P.M. RELATIVE TO DRUM R.P.M.
(Group 1)

	1	Postoperative Test No.		
		2	3	4
Forebrain Ablates	Mean (S.D.) -3.3 (± 1.5)	-4.2 (2.3)	-4.1 (1.9)	-2.7 (1.5)
Sham Operates	+2.2 (2.9)	+3.0 (2.1)	+2.6 (1.7)	+1.6 (1.2)

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

The ability of the fish to turn, either to the right or left side was not hampered. It did not matter which lobe of the forebrain was removed. When the entire forebrain was removed from a fish, the number of reversals dropped significantly as presented in table 6 and shown graphically in figure 7.

It would have been interesting to measure precisely reversal latency, but the equipment was not sophisticated enough to detect subtle changes.

TABLE 2
FISH R.P.M. RELATIVE TO DRUM R.P.M.
(Group 2)

	Preoperative Test No.			Postoperative Test No.			
	1	2	3	4	5	6	7 ^a
Forebrain Ablates ^b	Mean (S.D.) 0.9 (± 0.8)	1.8 (1.6)	2.0 (0.9)	-2.9 (2.0)	-4.2 (2.9)	-4.8 (2.5)	-1.2 (3.4)
Sham Operates	1.8 (1.0)	1.3 (1.5)	1.8 (2.0)	1.1 (1.3)	0.8 (2.6)	0.7 (1.4)	1.4 (2.8)

^a The seventh test took place one and one-half months after the sixth.

^b Ablation took place after test 3.

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

The impression was that latency, or the actual time it took the fish to turn, appeared to be the same in all groups.

VIOLENT BEHAVIOR: We designated as violent behavior a noteworthy behavioral alteration that occurred mainly among the forebrainless fish. The fish would thrash about very vigorously in the testing aquarium striking the sides, top, and bottom.

TABLE 3
FISH R.P.M. RELATIVE TO DRUM R.P.M.
(Group 3)

		Preoperative Test No.				Postoperative Test No.				
		1	2	3	4	5	6	7	8	9
Hemi-forebrain										
Ablates ^a	Mean									
	(S.D.)									
	0.7	1.6	3.7	-1.5	-1.7	-0.7	-0.4	-1.1	-2.4	
	(±1.5)	(2.0)	(2.8)	(3.4)	(3.7)	(3.6)	(3.5)	(3.5)	(3.3)	
Forebrain										
Ablates							-6.0	-6.0	-5.0	
							(1.6)	(3.0)	(2.1)	
Sham										
Operates	1.3	3.1	5.8	4.8	5.0	3.8	3.2	2.1	2.5	
	(1.6)	(1.7)	(1.6)	(1.6)	(1.7)	(1.9)	(1.2)	(1.3)	(1.0)	

^aHemi-forebrain ablation took place after test 3; forebrain ablation after test 6.

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

Sham operates showed violent behavior infrequently. For example, among Group 1 fish, at test 4, violent behavior occurred 0.07 and 0.1 times per test, respectively. In contrast, forebrainless fish were violent 1.4 times per test. We did not see violent behavior among Group 2 fish prior to ablations but it did occur later among forebrainless fish. Sham operates did not become violent at all, similarly, among Group 3 fish, sham operates never became violent, whereas hemi-forebrainless fish became violent 0.3 times per test and those entirely forebrainless, 0.8 times per test.

Other infrequent behaviors included eye nystagmus, swimming backwards in the direction of the drum, reversals not related to drum reversal, and sporadic swimming.

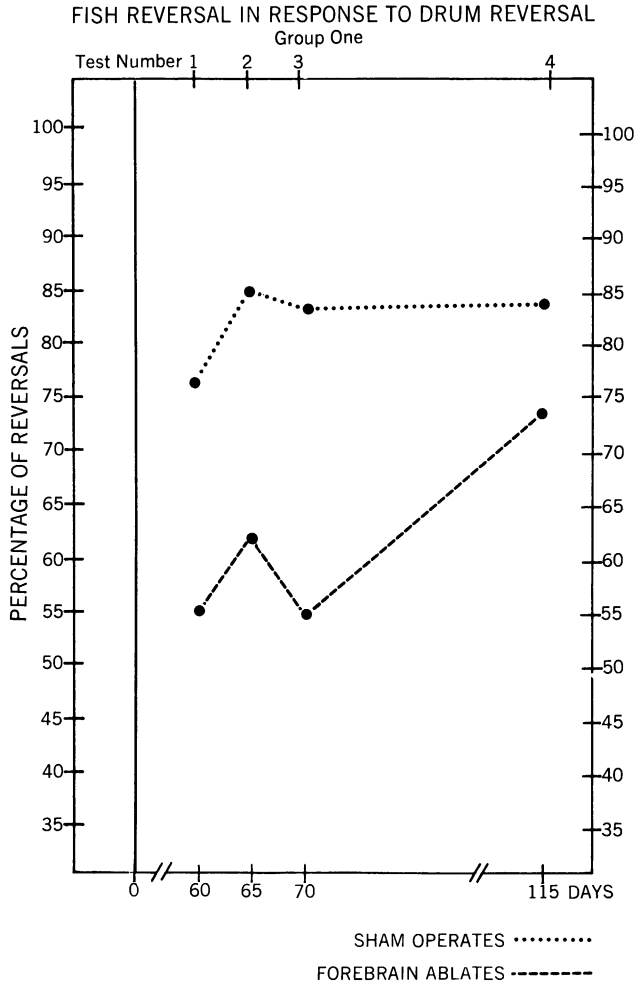


FIG. 5. Group 1. Drum was reversed 10 times, at end of each minute. Graph shows percentage of times fish reversed direction when drum direction was reversed. Vertical line indicates day of ablation.

DISCUSSION

The optomotor reaction of *T. mossambica* was affected by forebrain ablation. Although the optomotor response was not eliminated, modifications occurred.

Fish without forebrains showed significantly lower scores, neither turning as frequently, nor describing as many r.p.m. as the sham

TABLE 4
PERCENTAGE OF FISH REVERSAL IN RESPONSE TO DRUM REVERSAL
(Group 1)

	Postoperative Test No.			
	1	2	3	4 ^a
Forebrain Ablates	Mean (S.D.) 55 (\pm 31)	62 (33) ^a	55 (32)	72 (36)
Sham Operates	76 (23)	85 (35)	83 (33)	84 (29)

^aTest 4 took place one and one-half months after test 3.

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

operates. If only half the forebrain was removed, fish showed scores lower than those of the sham operates, but not so low as the total ablates. If we extend these findings to schooling behavior and consider features of the optomotor response to be similar to features of the schooling response (Shaw and Tucker, 1965), the following behavioral changes could be predicted in a school: A forebrainless fish in the school could maintain parallel orientation but would be unable to sustain appropriate swimming speeds, tending to fall behind the school. When the school executed a quick change in direction, the forebrainless fish probably would not change direction.

TABLE 5
PERCENTAGE OF FISH REVERSAL IN RESPONSE TO DRUM REVERSAL
(Group 2)

	Preoperative Test No.			Postoperative Test No.			
	1	2	3	4	5	6	7 ^a
Forebrain Ablates ^b	Mean (S.D.) 80 (\pm 33)	79 (31)	73 (34)	36 (17)	34 (27)	32 (17)	38 (25)
Sham Operates	90 (23)	88 (14)	76 (32)	82 (30)	79 (37)	72 (28)	78 (28)

^aTest 7 took place one and one-half months after test 6.

^bAblation took place after test 3.

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

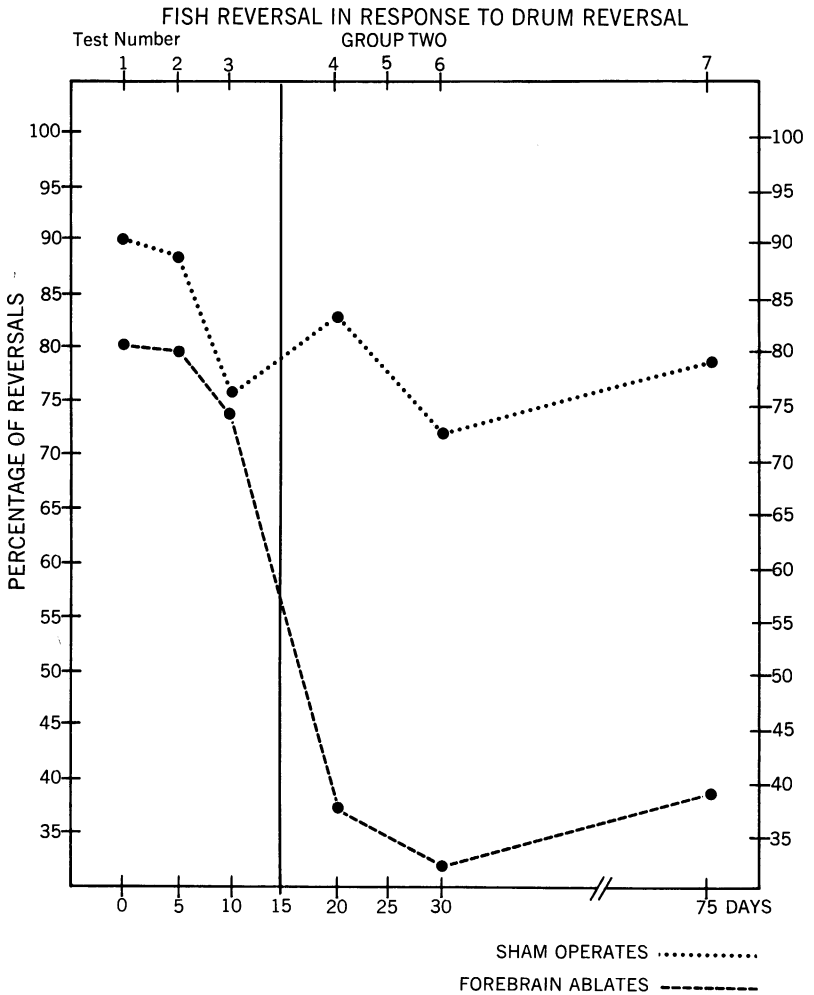


FIG. 6. Group 2. Drum was reversed 10 times, at end of each minute. Graph shows percentage of times fish reversed direction when drum direction was reversed. Vertical line indicates day of ablation.

Inability of forebrainless fish to change direction rapidly in response to change in direction of the school was reported by Noble (1936). Other researchers reported a sluggishness or slowness of reaction of forebrainless fish. Escape responses in *T. macrocephala* were often delayed, slow, or poorly oriented (Kaplan and Aronson, 1969) and sometimes the fish swam in the wrong direction. Forebrainless *Carassius auratus* were less

TABLE 6
 PERCENTAGE OF FISH REVERSAL IN RESPONSE TO DRUM REVERSAL
 (Group 3)

	Preoperative Test No.					Postoperative Test No.				
	1	2	3	4	5	6	7	8	9	
Hemi-Forebrain Ablates ^a	Mean (S.D.)									
	74 (±30)	96 (8)	99 (30)	54 (29)	64 (28)	75 (24)	97 (47)	93 (94)	93 (94)	
Forebrain Ablates ^b							42 (26)	54 (34)	64 (28)	
Sham Operates	81 (21)	99 (3)	95 (11)	86 (12)	97 (5)	90 (15)	90 (20)	93 (11)	93 (13)	

^a Hemi-forebrain ablation took place after test 3.

^b Forebrain ablation took place after test 6.

Vertical lines indicate significant differences between the experimental categories, Newman-Keuls, one-way analysis of variance, $p < 0.05$.

active (Dewsbury and Berstein, 1969), Hosch (1936) reported *Phoxinus sp.* and *Gobio gobio* (his *G. fluviatilis*) to be sluggish and to show a "loss of initiative." However, once the stimulus triggered a response, it consisted of rather violent movements, a matter to be discussed below. Kumakura (1928) reported a tendency of goldfish to remain motionless, at least at the beginning of the postoperative period, but they returned eventually to the schooling patterns of normal fish. Janzen (1933) tested goldfish in an optomotor apparatus, obtaining results that were diametrically opposed to ours: Occasionally, after ablation, the fish appeared to be completely adjusted to the stripes, following them consistently, whereas violent reactions appeared in normal fish. He did not mention whether the fish were slower or faster than the moving stripes, therefore an evaluation and comparison with his results are impossible. In addition, he was experimenting with the goldfish, and the differences in response may be attributable to species differences.

What functions can be proposed for the forebrain schooling behavior? In related studies, Dewsbury and Bernstein (1969) suggested that, "the forebrain facilitates the processing of information and coordination of behavior so that it is appropriate to external stimulus conditions" and "a decrease in ability to process information results in the animal ap-

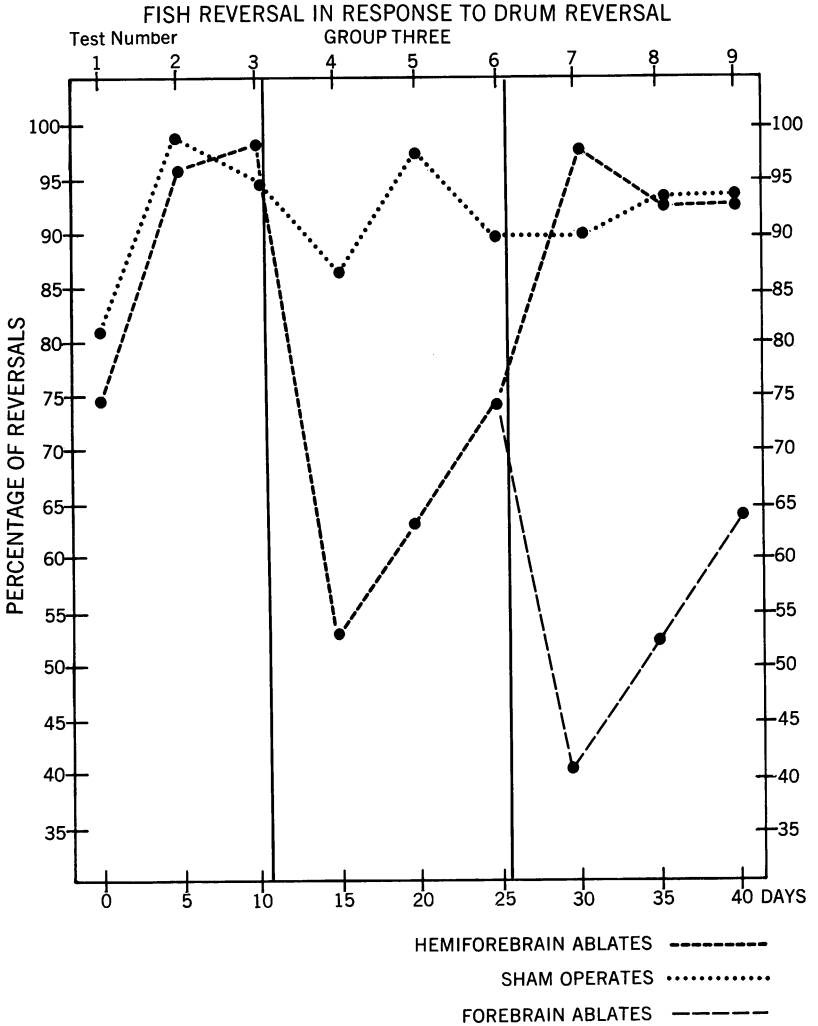


FIG. 7. Group 3. Drum was reversed 10 times, at end of each minute. Graph shows percentage of times fish reversed direction when drum direction was reversed. Vertical line after 10 days indicates day when one-half the forebrain was removed; after 25 days when the other half was removed from five of the 10 fish.

pearing less responsive." Aronson and Kaplan (1968) presented the hypothesis that the forebrain has a facilitatory role (including both inhibition and excitation) with respect to both the motor and sensory

processes mediated in lower brain centers. Schooling is an essentially visual phenomenon. Fish need to see in order to school and their adjustments within the school, such as the speed of swimming and change in direction are processed through the visual system (Shaw, 1970). We may wish to assume that the forebrain ablate is receiving the same sensory input in the visual cortex as before the operation. When the information is integrated in the intact animal, appropriate adjustments are made, but in the operated animal, integrative mechanisms are disturbed and appropriate adjustments cannot be made. The fish becomes unable to reverse direction readily in response to directional reversal of the drum.

The slowness of the fish in relation to the drum is somewhat more difficult to understand. Once oriented in the proper direction, the fish swim significantly fewer revolutions per minute than the drum and the sham operates. Is it possible that the forebrain serves to attune the fish to the r.p.m., allowing for precision in its timing relevant to the drum? As Shaw and Tucker (1965) mentioned, the fish, by maintaining an r.p.m. similar to drum r.p.m. and by taking a visual "fix" on a particular area, was essentially stopping the movement of the drum. However, if the fish lags behind, the stripes are always moving past its eye in a temporal-nasal direction and so the fish always has movement going past its eye. To have the stripes constantly moving would be a stressful condition, giving rise to a stressed fish and might, in fact, give rise to the bursts of agitated or violent behavior seen among forebrainless fish. If the forebrain, considered to have both excitatory and inhibitory functions, serves to keep the fish appropriately attuned to the environment, then its loss could serve as an explanation of violent behavior and the lack of ability to keep up with the stripes.

SUMMARY

The forebrain was removed from *Tilapia mossambica*, a cichlid fish that shows schooling behavior. The fish was tested in an optomotor apparatus before and after forebrain ablation. After ablation, there were significant decrements in fish r.p.m. in relation to drum r.p.m. and in the ability of the fish to reverse direction when drum direction was reversed.

The relevance of these findings to schooling is discussed.

ACKNOWLEDGMENTS

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