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BEHAVIORAL CORRELATES OF CEREBELLAR ABLATIONS IN THE TELEOST FISH, *AQUIDENS LATIFRONS*

Jack Izower and Lester R. Aronson

ABSTRACT: The effects of ablation of the corpus, eminentia granularis and valvula of the cerebellum on the performance of optomotor tasks, and the appearance of atypical behavior patterns were studied in the teleost fish *Aquidens latifrons*. The subjects were observed in their home tanks before and after surgery, and were tested in a modified optomotor apparatus where the drum changed direction of rotation at regular intervals. The corpus cerebellum was ablated totally or partially, bilaterally or unilaterally. In other subjects the eminentia granularis was ablated on the right side or in conjunction with ipsilateral corpus lesions. The valvula was completely ablated in still other subjects with only slight damage to adjacent brain tissue.

When experimentally naive intact fish were given a series of optomotor tests they gradually improved their optomotor performance. After cerebellar operations this improvement was reversed in most of the optomotor measurements as the fish followed the moving stripes much less efficiently. However swimming speed, which we considered a good indicator of motor performance, was unchanged except in 2 out of 13 groups. We concluded that the less efficient optomotor behavior could not be attributed to a direct effect of the lesions on motor processes. The home-tank observations clearly revealed four postoperative motor abnormalities. Oscillatory movements, wobbling and tilting persisted through the tests, but the fourth, lying on the side, a more profound disability, disappeared in all but one subject in a few hours to a few days. The first three abnormal behavior patterns, especially the oscillatory movements, suggest a deficiency in fine motor tasks and support the interpretation that the major function of the cerebellum is described best as the modulation of movement.

High levels of tilting and lying on the side in subjects with unilateral lesions may be caused by an inbalance in motor function. Several alternative or additional functions of the cerebellum suggested by these experiments are evaluated.

INTRODUCTION

Relatively little attention has been paid in recent years to the function of the cerebellum in teleost fishes. This contrasts with the rather considerable effort to understand the functioning of the forebrain. Two reasons for this discrepancy are suggested. First, thoughts concerning the functions of the teleost cerebellum have been influenced by its basic structural similarity to the cerebelli of most other vertebrates, leading to the assumption that its functions are also similar (Ingvar, 1928; Llinas and Hillman, 1969; Finger, 1978). Hence there is less interest in exploring the function of this

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part of the brain in these vertebrates. Secondly, methods adequate for quantitative studies of cerebellar motor and nonmotor functions in fishes have hardly been developed or utilized (e.g. Nolte, 1933; Tuge, 1934; Karamian, 1956). The present study addresses both of these potential problems.

Previous investigations of fish neurology have ascribed a variety of functions to the cerebellum: control of posture, locomotion and equilibrium, coordination and fine control of movements, muscle tone, integration of proprioception, sensory processing and learning (reviewed by Healy, 1957; Dow and Moruzzi, 1958; Aronson, 1963; Kaplan and Aronson, 1969; Bernstein, 1970 and others).

Several authors have reported severe motor deficiencies following cerebellar lesions, suggesting that cerebellar function in teleosts really is similar to that of other vertebrates (Dow and Moruzzi, 1958; Fadiga and Pupilli, 1964; Goodman, 1964, 1969). Other investigators have reported only minimal and mostly transient motor defects even when all of the body of the cerebellum has been ablated (Loeb, 1900; Polimanti, 1912; Aronson, 1948; Kaplan and Aronson, 1969 and others). They have emphasized sensory and learning functions for this part of the fish brain despite its morphological similarity to the mammalian cerebellum where many studies have shown that the predominant function is the control or modulation of movement. Nonmotor functions, especially learning, have also been described in mammals and other lower vertebrates (Watson, 1978). Karamian (1956) proposed that classical (Pavlovian) conditioning plus a trophic process were major functions of the cerebellum in fishes and that during the course of evolution, the establishment of the connection in these conditioned reflexes transferred from the cerebellum to the forebrain in amphibia and higher vertebrates.

To throw additional light on these questions we used a uniquely modified optomotor test, an analysis of swimming behavior and systematic home-tank observations of undisturbed fish to provide a quantitative picture of the effects of a variety of cerebellar lesions and ablations.

METHODS

Subjects and Apparatus

Aquidens latifrons (Steindachner), 6-9 cm. long, were selected from laboratory stock. Each fish was individually housed in a 13-liter aquarium visually isolated from all other fish. Subjects for the preliminary experiments were housed in a greenhouse. For the main experiment the fish were housed in a laboratory room where they were exposed to constant light and were not disturbed except for feeding and testing.

The optomotor device consisted of two concentric plexiglass cylinders. The transparent inner cylinder, which was filled with water and held the subject being tested, was 14 cm. high and 15 cm. in diameter. The outer cylinder, 20 cm. in diameter, was opaque and covered with alternating black and white vertical bands, 1.5 cm. wide, each subtending a 15° angle. The drum rotated at 20 RPM, and the direction of rotation was reversed at regular intervals following the design of Shaw and Sherman (1971). The apparatus was housed in a cabinet illuminated by an overhead 25W circular fluorescent light. An overhead mirror tilted at a 45° angle enabled the observer to view the fish, but the observer, seated in a darkened room was not visible to the subject.

In the preliminary experiments the behavioral components of the optomotor response were encoded and collected with the aid of a modified SCM electric typewriter. For the main experiments a computer keyboard was used for encoding the data. Different characters were used to represent the behavior patterns described below. The preliminary data were analyzed statistically by hand but computer programs were used for analysis of the main experiment.

Optomotor Tests—Behavioral Parameters and Procedures

Eight behavioral parameters were used: (1) Initial latency (init. lat.)—the elapsed time after a change in drum rotation until the subject started to follow the new direction of the drum either by swimming backward or by turning and swimming forward. (2) Turn latency (turn. lat.)—the interval between reversal of the direction of drum rotation and the time that the fish turned and swam forward in the new direction. (3) Swimming speed (swim. spd.)—the number of times that a steadily swimming subject passed a marker between the 30th and 45th sec. of the trial (560 cm. to 750 cm. per minute). Swimming speed is a measure of gross locomotor activity and is a likely indicator of the physical condition of the subjects. (4) Forward turning frequency (for. turn.)—number of times that the subject reversed direction in order to follow the changed direction of the rotating drum. (5) Forward following duration (ford. folw.)—total time that the subject followed the drum while swimming in the direction of rotation. (6) Stationary duration (stat. dur.)—sum of the intervals of time in which the subject was stationary while the drum was revolving. (7) Opposite swimming duration (opp. swim.)—total time that the fish swam counter to the direction of drum rotation. (8) Backward swimming duration (back. swim.)—total time the fish followed the drum while swimming backward, i.e. tail first.

Five minutes prior to the optomotor test the subject was placed in the inner cylinder of the optomotor device. This accustomed the fish to the surroundings. The optomotor device was rotated initially in a clockwise direction. Every 56 seconds the direction of rotation was reversed automatically. Data of the first trial were disregarded since the fish were not uniformaly oriented when this trial started. In subsequent trials the fish were usually oriented in the same direction because in the previous trial they had been swimming in the direction of drum rotation. The daily score for each fish was the average of ten trials, five in each direction. In the occasional trial where the fish turned around before the trial ended and was therefore facing counter to the direction of drum rotation, the data for the next trial were excluded because the fish were already facing in the new drum direction at the start of the trial.

Testing Protocol—Optomotor Tests

Intact fish from community tanks were isolated for three days prior to the test. They were then tested once a day (11 trials per test) in the optomotor apparatus for six consecutive days. Fish that failed to respond to the moving stripes by the second test day (about 10%) were excluded. Following these tests operations were performed using suction to make the lesions. Five days later the fish were retested once daily for six consecutive days. They were always tested in the same sequence and were fed after the tests. The results of the first day for each series of fish were discarded.

Home-Tank Observations and Procedures

Each day prior to the optomotor test, the fish were observed in their home tanks from behind a screen in a darkened section of the room. Five observations were made on each fish in both the preliminary and main experiments. Each observation lasted for 30 sec. during which the following deviations in locomotion and posture were often seen after various cerebellar lesions. (1) Oscillatory movements—regular movements, to and fro about 1 cm. along the longitudinal axis of the fish. (2) Wobbling—an unsteady side to side rocking motion while swimming. (3) Tilting—leaning to one side while the fish were stationary; sometimes a ventral fin touched the substrate. (4) Lying on side—The fish were observed lying on one side. Sometimes the body was rigid and in an almost U-shaped curve, at other times the head and tail touched the substrate and the body was arched.

Testing Schedule

In preliminary groups I and II, the fish were tested in the optomotor device on preoperative days 1-5 and were observed in the home tank on days 25-29. Optomotor tests were made on postoperative days 10-14 and for group I additional tests were run on days 56-60. Home-tank observations were performed on postoperative days 2-6, 23-27 and for group I an additional series on days 56-60. In preliminary group III, the intact control animals were tested on preoperative days 1-5 and again on days 11-15 in both the home tank and optomotor apparatus. Additional home-tank observations were made on days 5-10. These subjects were then transferred to group IV of the main experiment where postoperative home-tank observations were made on days 1-20. Postoperative optomotor tests were performed on days 6-10 and 16-20.

In the remaining groups of the main experiment (V-XIII) preoperative home-tank and optomotor observations were made on days 1-5. Postoperative home-tank observations were made on days 1-5 and 6-10 while postoperative optomotor tests were performed on days 6-10.

Statistics

Optomotor measurements were analyzed with a repeated measures analysis of variance with unequal numbers of subjects (Winer, 1971). Comparisons between day five means and the scores for each day were made with the Student-Newman-Keuls procedure (Sokol and Rohlf, 1969).

Home-tank behavior was analyzed by a repeated measures analysis of variance (Edwards, 1968). Comparisons within each operation were made by using the Scheffe' Multiple Comparison test (Winer, 1971).

Histology

All of the fish were sacrificed at the end of the testing period; the brains were sectioned at 15 mu. and stained with gallocyanin. A series of outline drawings of the lesions based on the histology were made for all subjects and from these, the final composition of the groups were established. The data of the main experiment were not examined until the final composition of the groups were made. A typical example for each group is given in figures 1 and 2.

RESULTS

Optomotor Experiments

Prior to surgery several of the behavioral measurements changed gradually between the first and fifth test. When these preoperative data for 10 of the groups were pooled (n=63), Izower and Aronson (1980) found

Table 1
Preliminary Experiments—Optomotor Behavior

Treatment Group	*Days*	*init. lat. (sec)* [a]	*turn. lat. (sec)*	*ford. folw. (sec)*	*stat. dur. (sec)*	*opp. swim. (sec)*	*for. turn. freq.* [b]	*swim. spd. RPM*	*back. swim. (sec)*
I sham operate n=8	PR.5 [c]	8.2	10.0	45.7	4.5	3.5	9.4	4.4	5.8
	PO.10-14	7.5	11.2	41.9	4.2	5.2	10.0	4.8	6.7
	SIG	0	0	0	0	0	0	0	0
	PO.56-60	6.7	9.4	41.1	3.7	3.3	9.9	4.9	6.1
	SIG	0	0	0	0	0	0	0	0
II total corpus ablates n=8	PR.5	8.6	13.1	41.5	6.3	4.5	9.8	4.6	6.6
	PO.10-14	17.8	22.8	28.0	11.3	10.9	8.8	4.2	14.4
	SIG	3	3	5	1	5	1	0	3
III [d] intact control n=7	PR.5	6.8	13.6	42.8	3.2	1.7	10.0	3.3	6.2
	PO.11-15	5.6	14.6	39.9	2.5	2.0	9.9	2.9	9.5
	SIG	0	0	0	0	0	0	0	0

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[a] See page 30 for description of behavior and key to abbreviations.

[b] Mean number of turns during test period based on ten drum reversals per test.

[c] The preoperative (PR) day five values are averages for that day. The postoperative (PO) values are for five days. SIG is the number of days that the postoperative values were statistically different at the .05 level from the preoperative day five value (Student-Newman Keuls test, Sokoll and Rohlf, 1969).

[d] For comparisons of control group III with groups IV to XIII, preoperative (PR) days 11-15 is the equivalent of postoperative (PO) days 6-10.

that initial latency, turn latency, duration of opposite swimming and the duration of stationary stance decreased gradually over the five days of testing so that the fifth day averages were significantly lower than the first day. On the other hand, forward following increased significantly during this period. Swimming speed, frequency of forward turning and backward swimming did not change. Because of the gradual changes in preoperative behavior, we used the average score of the fifth day of testing of the intact fish for comparison with the postoperative scores.

Preliminary Experiments

Group I—sham operates. After removal of the cranium directly above the cerebellum we found no significant changes in any of the eight optomotor behavior patterns in two series of postoperative tests.

Group II—total corpus ablation. After the operation there was a significant increase on one to five days in initial latency, turn latency, stationary stance, opposite swimming and backward swimming. Forward following declined on all days, but the changes were significant on only one day. Swimming speed was not significantly affected by the operation.

Group III—intact controls. This group was included to determine whether there would be additional changes in preoperative behavior after those observed in the first five days of testing. We therefore allowed a five day rest period after day five and then retested the fish daily on days 11-15 which were equivalent to days 1-5 in all groups of the main experiment. No statistically significant changes in any behavior occurred. Thus changes in behavior after surgery in the subsequent groups can be attributed to the operations and not to the retesting procedure.

Main Experiments

Group IV—total corpus ablated (Table 2, Figure 1). The subjects in this group were given two series of postoperative tests on days 6-10 and 16-20. The results were similar to those of group II. In the second series of tests the postoperative changes were more pronounced.

Group V—caudal corpus totally ablated, rostral corpus largely ablated (Table 2, Figure 1). In this group and in all subsequent groups, just one series of postoperative tests were given on days 6-10. The effects of this operation were very similar to those of groups II and IV.

Group VI—rostral corpus mostly ablated bilaterally; caudal corpus ablated on right side (Table 2, Figure 1). The performance of this group

Table 2
Main Optomotor Experiments—Corpus Ablations

Treatment Group	*Days*	*init. lat. (sec)* [a]	*turn. lat. (sec)*	*ford. folw. (sec)*	*stat. dur. (sec)*	*opp. swim. (sec)*	*for. turn. freq.* [b]	*swim. spd. RPM*	*back. swim. (sec)*
IV [d] total corpus X n=7	PR. 5 [c]	6.8	13.8	42.8	3.2	1.7	10.0	3.3	6.2
	PO.6-10	18.5	21.7	32.4	11.0	5.5	9.2	3.1	5.1
	SIG	5	0	3	5	3	0	0	0
	PO.16-20	15.5	23.8	24.4	14.6	8.8	7.9	3.2	6.1
	SIG	5	1	5	5	5	5	0	0
V rostral mostly X; right caudal X n=4	PR.5	8.3	15.3	40.3	3.2	3.6	10.0	3.1	6.2
	PO.6-10	15.8	18.2	28.1	10.5	11.1	8.4	2.9	3.2
	SIG	5	0	5	5	5	3	0	0
VI rostral mostly X; total caudal X n=5	PR.5	7.1	9.5	44.9	2.3	2.6	10.0	2.8	3.2
	PO.6-10	11.0	13.3	33.3	9.3	7.2	8.6	2.6	2.2
	SIG	0	1	2	2	2	3	0	0
VII right total X; left intact n=8	PR.5	7.2	17.1	37.8	3.5	2.4	9.9	2.9	9.9
	PO.6-10	11.0	15.8	32.1	8.1	6.4	9.6	2.9	6.6
	SIG	1	0	1	3	3	0	1	0
VIII right superfic left intact n=5	PR.5	7.4	10.2	44.7	2.5	2.6	10.0	3.2	3.3
	PO.6-10	6.1	10.1	37.6	4.3	1.9	9.5	2.8	8.9
	SIG	0	0	0	0	0	0	0	2

[a-c] See Table 1 for explanation of these footnotes
[d] X=extirpation.

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was similar to that of groups II, IV and V but the differences were only significant on one to three days.

Group VII—right side of corpus completely ablated (Table 2, Figure 1). Initial latency, stationary stance and opposite swimming all increased,

Figure 1

Cross sections through the cerebellum and tegmentum of operated fish showing extirpated areas of the brain in stippling. One sample was selected for each group in the main experiment. The letters indicate the level of the sections from A, anterior to L, posterior. The numbers refer to the anatomical list on p. 36.

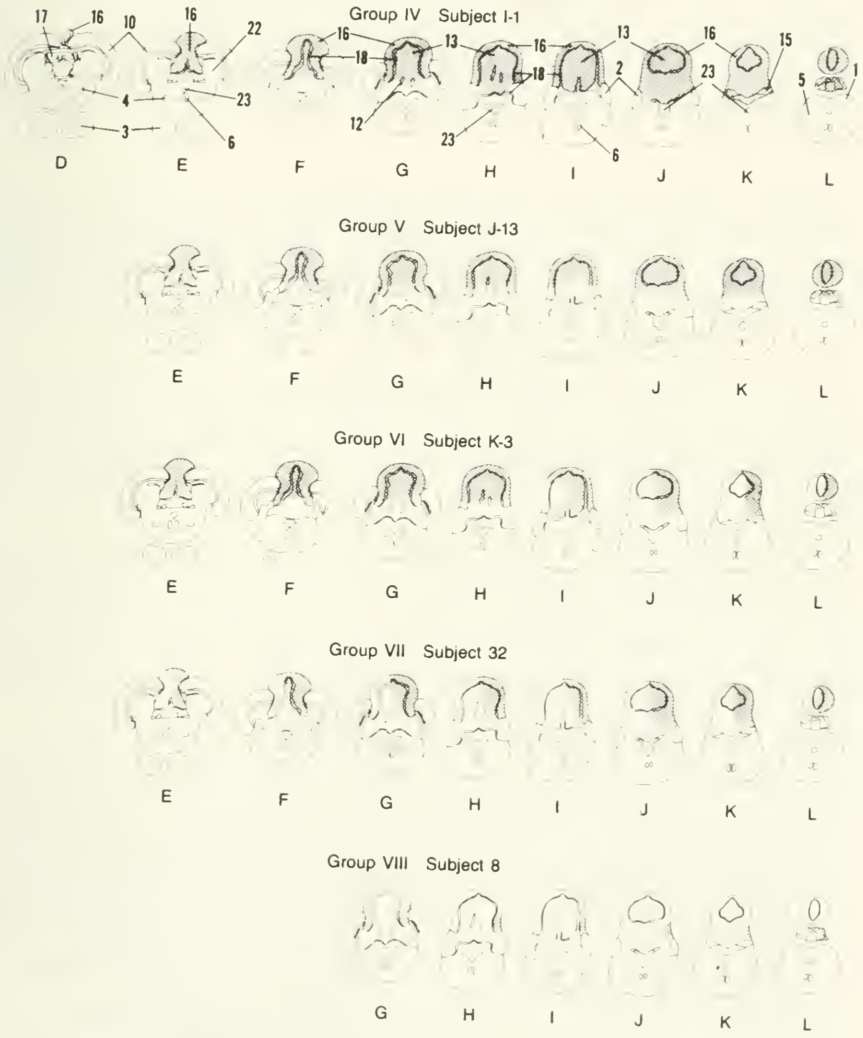
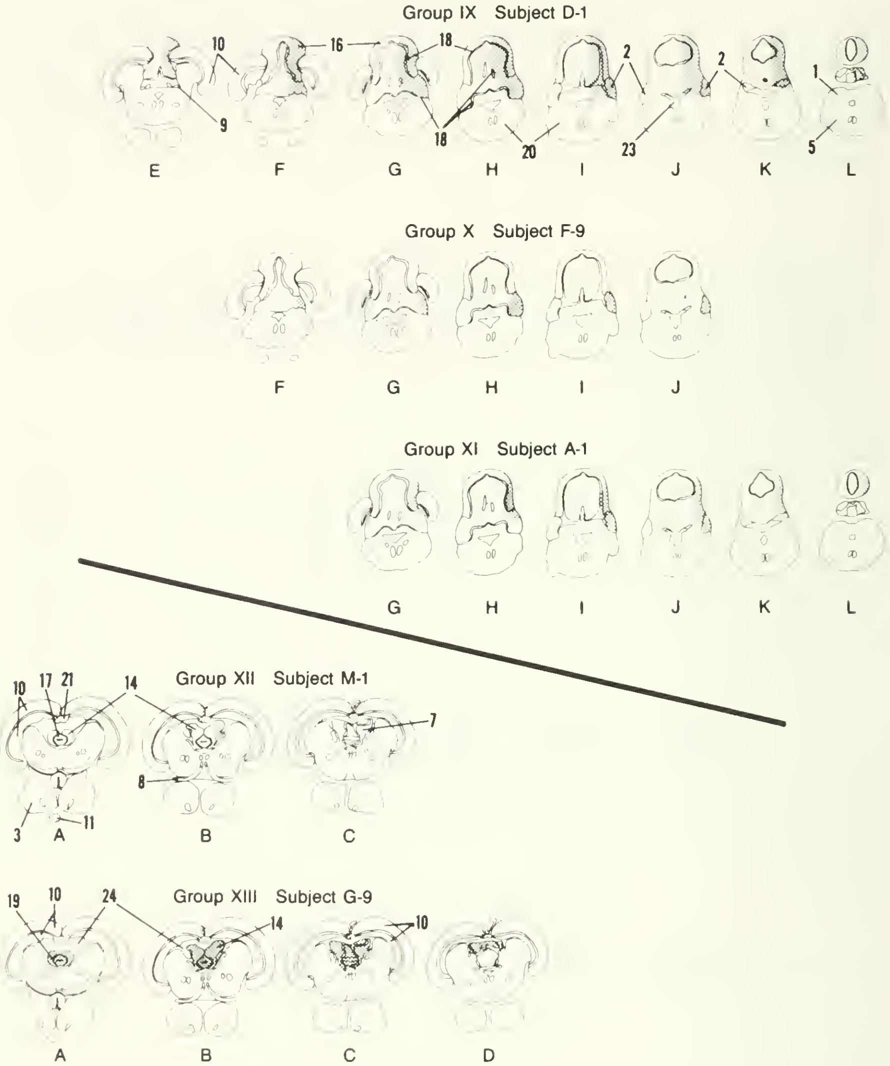


Figure 2



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1 crista cerebellaris
2 eminentia granularis
3 inferior lobe hypothalamus
4 lateral lemniscus
5 medulla oblongata
6 median longitudinal fasciculus
7 nucleus valvula lateralis
8 nerve 3
9 nerve 4
10 optic tectum
11 saccus vasculosus
12 stratum fibrosum corpus cerebelli
13 stratum granulare corpus cerebelli
14 stratum granulare valvula
15 stratum granulare ventralis
16 stratum moleculare corpus cerebelli
17 stratum moleculare valvula
18 stratum Purkinje corpus cerebelli
19 stratum Purkinje valvula
20 tegmentum of mesencephalon
21 torus longitudinalis
22 torus semicircularis
23 ventricle 4
24 optic ventricle

Key to Labels of Brain Sections

forward following, swimming speed and backward swimming decreased while turn latency remained unchanged. These changes were similar in direction to those preceeding groups having extensive corpus lesions (groups II, IV, V, VI).

Group VIII—superficial lesion of the right corpus (Table 2, Figure 1). The shallow lesions in these fishes did not cause significant changes in any measure except for an unexplained increase in backward swimming.

Group IX—ablation of the right corpus and right eminentia granularis (Table 3, Figure 2). This operation caused major changes in optomotor behavior very similar to total or extensive lesions in the corpus. Compared to ablation of the right corpus alone (group VII), the changes were much more pronounced.

Group X—total ablation of right eminentia granularis (Table 3, Figure 2). This operation resulted in a significant decline in forward turning on all five days, and a drop of forward following that was significant on four days. Stationary stance increased considerably. There was a substantial decrease in opposite swimming but this was not significant on any day.

Group XI—partial ablation of right side of caudal eminentia granularis and partial ablation of right side of corpus (Table 3, Figure 2). The deficits were less severe than for the total unilateral ablation of these structures in group IX.

Group XII—small medial lesion in optic tectum (Table 3, Figure 2). This group served as a control for the valvula ablations (group XIII) since access to the valvula depended on cutting through the midline between the optic tecta. These small lesions did not affect the performance of the subjects.

Group XIII—valvula totally ablated (Table 3, Figure 2). Initial latency, turn latency, stationary duration and backward swimming increased significantly after the operation while forward following decreased significantly on four days. Changes in optomotor behavior after destruction of the valvula were similar to total removal of the corpus (compare with groups II, IV).

Home-Tank Behavior

Preliminary observations of behavior in the home tanks following a variety of cerebellar lesions revealed several abnormalities in posture and locomotion as described in the methods section. The frequency of these abnormal behaviors were recorded for the 13 groups. Since no behavioral

Table 3
Main Optomotor Experiment—Additional Ablations

Treatment Group	*Days*	*init. lat. (sec)* [a]	*turn. lat. (sec)*	*ford. folw. (sec)*	*stat. dur. (sec)*	*opp. swim. (sec)*	*for. turn. freq.* [b]	*swim. spd.* RPM	*back. swim. (sec)*
IX [d]									
right	PR. 5 [c]	6.0	10.0	45.9	3.0	1.3	10.0	3.2	13.1
corpus X;									
right	PO.6-10	13.2	16.7	28.3	13.2	6.6	8.1	2.8	6.9
eminent X	SIG	5	1	5	5	4	5	1	0
n=6									
X									
right	PR.5	8.0	11.3	44.8	1.9	4.1	10.0	3.4	4.1
eminent X									
n=4	PO.6-10	8.5	10.7	34.2	9.0	3.2	8.4	3.4	3.1
	SIG	0	0	4	2	0	5	0	0
XI									
right	PR.5	7.6	11.9	42.5	3.0	2.4	9.7	3.1	5.3
corp partl									
rt emnt X	PO.6-10	10.5	18.0	32.9	4.3	5.8	9.2	3.4	10.0
n=7	SIG	0	1	4	0	2	0	0	0
XII									
midline	PR.5	5.4	8.9	46.5	1.4	2.2	10.0	3.2	4.1
cut-tectm									
	PO.6-10	4.7	7.6	48.1	1.3	1.6	10.0	3.2	3.1
n=9	SIG	0	0	0	0	0	0	0	0
XIII									
valvula	PR.5	5.4	10.2	45.5	1.3	1.8	10.0	3.2	5.0
ablation									
n=8	PO.6-10	9.1	17.0	37.3	5.3	2.5	9.6	3.0	8.4
	SIG	2	3	4	1	0	0	0	1

[a][c] See Table 1 for explanation of these footnotes
[d] X=extirpation.

abnormalities were seen in any of the preoperative tests, the postoperative data described below represents changes resulting from the operation.

Preliminary Experiment

Group I—sham operates (Table 4). During most of the observations these fish maintained an upright posture and smooth balanced and well-controlled swimming. Just an occasional wobble and tilt ($< 1\%$) were recorded. There were no oscillatory movements or resting on side.

Table 4
Postoperative Home-Tank Behavior—Bilateral Lesion Groups [a]

Treatment Groups [b]	*Post-Operative Days*	*Oscillatory Behavior*	*Wobbling*	*Tilting to Side*	*Lying on Side*
I sham operate n×8	2-6	0	1	1	0
	23-27	0	0	1	0
	56-60	0	1	0	0
II total corpus X n×8	2-6	39	23	6	0
	23-27	36	15	8	0
IV total corpus X n×7	1-5	43	7	14	0
	6-10	33	6	11	0
	11-15	45	6	10	0
	16-20	49	6	1	0
V rostral corpus mostly X; rt. caudal corpus X n×4	1-5	23	27	4	2
	6-10	6	13	10	1
VI rostral corpus mostly X; total caudal X n×5	1-5	4	3	23	1
	6-10	4	2	13	0
XII midline cut in tectum n×9	1-5	2	0	9	0
	6-10	0	0	1	0
XIII valvula n×8	1-5	6	1	11	14
	6-10	4	0	3	0

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[a] Percent of frequencies for five 30 sec observations for five daily tests for all the subjects in the groups.

[b] These behavior patterns were rarely observed in the unoperated fishes. Since the values for group III and the preoperative data for all groups are close to zero, they have been omitted.

Group II—total corpus ablation (Table 4). Oscillatory movements were seen in 39% of the first series of observations and 36% of the second. Tilting remained at a low level for both test series. Lying on side was not observed.

Group III—intact controls. As noted previously this group was needed to determine whether continued testing after the initial preoperative series would cause further behavioral changes. Since the tests on days 6-10 and 11-15 were equivalent to the first and second postoperative tests in all the other groups, and since no postural or locomotor changes were observed, we are confident that the motor abnormalities seen after the operation were the result of brain damage.

Main Experiment

All of the groups were given two series of postoperative observations on days 1-5 and 6-10 with the exception of group four where there were two additional series on days 11-15 and 16-20.

Groups IV to VIII—the operations in these groups represent a graded series of decreasing severity of corpus deprivations. Oscillatory behavior which was very high after total corpus ablation—group IV (Table 4) declined gradually to a low level in group VIII (Table 5). Wobbling was variable and inconsistent. Tilting remained substantial even when the lesions were minimal and with one exception there was only a moderate decline in the second series of tests. Lying on side was low in groups V and VI (Table 4) but higher in groups VII and VIII (Table 5). We will return to this interesting difference later (p 000).

Groups IX, X, XI—(Table 5). The operations in these groups involved the right eminentia granularis. There was a moderate amount of oscillatory movements and wobbling but tilting to the side was high with only partial recovery in the second test series. Lying on the side was also high, but recovery in the second series was complete in all three groups.

Groups XII, XIII—(Table 4). In the first of these groups a dorsal mid-line lesion was made in the tectum. This served as a control for group XIII where the same lesion was needed to expose the valvula. Wobbling and lying on side were not seen; there was a low level of oscillatory movements and some tilting. After ablation of the valvula we observed moderate levels of tilting and lying on side and low levels of oscillatory movements and wobbling.

Examination of Tables 4 and 5 show that in 37 cases (71%), the scores in the second postoperative series were lower than in the first series. In just four cases (8%) did the scores go up in the second series and three of these four were in tilting. These results indicate an extensive recovery of cerebel-

Table 5
Postoperative Home-Tank Behavior—Unilateral Lesion Groups [a]

Treatment Groups [b]	*Post-Operative Days*	*Oscillatory Behavior*	*Wobbling*	*Tilting to Side*	*Lying on Side*
VII right total X; left intact n×5	1-5	13	10	22	5
	6-10	2	3.5	30	0
VIII right corpus superficl lesion n×5	1-5	3	4	14	19
	6-10	1	1	11	0
IX rt. corp. X rt. emn X n×6	1-5	13	8.5	14	45
	6-10	1.5	3.5	6	0
X rt. emn X n×4	1-5	0	5	45	17
	6-10	1.5	0	44	0
XI rt. corp. partl X; rt. emn X n×7	1-5	9	7	15	9
	6-10	1	1.5	14	0

For explanation of footnotes see Table 4.

lar function but this was much less pronounced after total corpus ablations (groups II and IV—Table 4). Particularly impressive was the high incidence of oscillatory behavior.

Also of interest is the striking difference between the unilateral and bilateral operations. In the unilateral groups (VII through XI—Table 5) tilting and lying on side were considerably higher than in the bilateral groups. The only exception to this is group VI, but here the lesion is considerably greater on the right side. In group VIII where there is just a superficial lesion on the right side, 19% of the first series of observations showed lying on the side which as noted previously was the most pronounced of the motor abnormalties. In contrast to this, after total, bilateral corpus ablation no lying on side was seen.

DISCUSSION

Optomotor Efficiency

The preoperative data for the main experiment were analyzed in an earlier report (Izower and Aronson, 1980) which showed that consistent quantitative changes occurred in several of the optomotor responses when the experimentally naive subjects were given their first series of tests. The scores for the last (fifth) tests were consistently different from the first tests. Thus, initial and turn latencies decreased, as did opposite swimming and stationary stance. On the other hand, forward following increased. We suggested that as the naive fish gained optomotor experience their performance improved in that they followed the moving stripes more accurately and effectively. That is, shorter latencies, less time spent not moving or swimming backward (tail first) or in the wrong direction, and the more time spent following in the right direction all suggest improvement in what we are calling optomotor efficiency. Only swimming speed, forward turning and backward swimming did not change consistently with experience.

Effects of Cerebellar Lesions

When preoperative data for day five were compared with the sham operates (group I) on postoperative days 6-10 and 56-60, no significant differences were seen in any of the optomotor scores. In subjects with cerebellar lesions, when the preoperative and postoperative scores were examined for the major optomotor parameters, namely, initial latency, turn latency, stationary behavior, opposite swimming, forward following, and to a lesser extent forward turning changes occurred which were opposite to the initial optomotor improvements discussed above for the intact fish. In essence, optomotor efficiency declined following almost all cerebellar ablations except in group VIII where the lesions were superficial (Table 6).

The cerebellum consists of several anatomically discrete parts (corpus, valvula, eminentia granularis and caudal or vestibular lobe) but, as noted above, our optomotor data did not identify any functionally localized areas. The eminentia granularis is a possible exception since removal of this structure on one side (group X) caused a pronounced decline in forward turning. Note also that this operation had no effect on the two latency measures. Unfortunately, the subjects given bilateral eminentia lesions all died during or shortly after the operation and we did not have the opportunity to perform serial lesions, which may have improved survival.

Morphological studies (Larsell, 1967; Nieuwenhuys, 1967) indicate that the valvula is a forward extension of the corpus. Our observations

Table 6
Trends in Optomotor Efficiency After Cerebellar Ablation [a] (Based on Data in Tables 1-3)

Group / Behavior	INTACT [b]	I	II	IV		V	VI	VII	VIII	IX	X	XI	XII	XIII
				6-10	16-20									
Init. lat.	↑ [c]	↔	↓ 2	↓ 5	↓ 5	↓ 5	↓ 1	↓ 1	↔	↓ 5	↔	↓ 0	↔	↓ 2
Turn. lat.	↑ [c]	↔	↓ 3	↓ 0	↓ 1	↔	↓ 1	↔	↔	↓ 1	↔	↓ 1	↔	↓ 3
Ford. follw.	↑ [c]	↔	↓ 5	↓ 3	↓ 5	↓ 5	↓ 2	↓ 1	↔	↓ 5	↓ 4	↓ 4	↔	↓ 4
Stat. dur.	↑ [c]	↔	↓ 1	↓ 3	↓ 5	↓ 5	↓ 2	↓ 3	↓ 0	↓ 5	↓ 2	↓ 0	↔	↓ 1
Opp. swim.	↑ [d]	↔	↓ 5	↓ 3	↓ 5	↓ 5	↓ 2	↓ 3	↑ 0	↓ 4	↑ 0	↓ 2	↑ 0	↓ 0
Ford. turn.	↔ [e]	↔	↓ 1	↔	↓ 5	↓ 3	↓ 3	↔	↔	↓ 5	↓ 5	↔	↔	↔
Swim spd.	↔ [e]	↔	↔	↔	↔	↔	↔	↓ 1	↔	↓ 1	↔	↔	↔	↔
Back swim.		↔	↓ 3	↔	↔	↑ 0	↑ 0	↑ 0	↓ 2	↓ 1	↓ 0	↓ 0	↑ 0	↓ 1

[a] For explanation of the term "optomotor efficiency" see p 42. Vertical arrows indicate increases (↑) or decreases (↓) in optomotor efficiency after operations. Numbers to the right of the arrows are the number of days (maximum × five) that the postoperative changes were significant at the .01 level. When the number is zero, the vertical arrows indicate average postoperative changes greater than 20%. The horizontal arrows are changes of 20% or less (i.e. the equivalent of no change).

[b] Based on the pooled preoperative data of ten of the groups (n×63). Data from Izower and Aronson (1980).

[c] $p < .01$

[d] $p < .05$

[e] $p > 0.5$

support this view in that ablations of the valvula and lesions of the corpus caused rather similar behavioral changes. In the mormyrids where the valvula is greatly hypertrophied this enlargement is correlated with the complex weakly electric apparatus that these fish are noted for (Russell and Bell, 1978). In the weakly electric ictalurids (cat fishes) electroreceptive areas were found mainly in the caudal lobe and to a minimal extent in the corpus and eminentia granularis but not in the valvula (Tong and Bullock, 1982). It is likely that electric function and associated valvular hypertrophy is a recent specialization and may have arisen in several independent lines of bony fishes whereas the original functions were similar to the corpus. This view is also supported by the work of Karamian (1956) and Bianki (1963) who reported that ablation of the corpus plus valvula in the crucian carp caused greater deficits in the formation of conditioned reflexes than ablation of the corpus alone.

The striking loss of optomotor efficiency after the various cerebellar lesions might be attributed to postoperative trauma, but this possibility is minimized by the behavior of the sham operates where no losses occurred. Also in group IV where the subjects were given a second series of postoperative tests on days 16 to 20, there were no signs of improvement. The lesions may have had a direct effect on motor function, but swimming speed, which we thought would be sensitive to motor dysfunction was hardly affected by any of the operations. Backward swimming was somewhat inconsistent but it did suggest a decrease in optomotor efficiency giving further support to our conclusion that the decline in optomotor efficiency was not due to the inability of the fish to swim normally or even backwards.

In birds and mammals the counterpart of the teleost optomotor response is the optokinetic reflex. Whereas in fishes the subject tends to swim in the direction of the moving background (e.g. vertical stripes), in birds just the head and neck move and in mammals just the eyes move, while the body remains stationary. Since eye movements in a given direction is limited (e.g. 15° horizontal in rabbits, Collewijin, 1970) the eyes reset rapidly to their original position and the reflex is repeated. This dual eye motion or oscillation is called optokinetic nystagmus. A variety of studies (summarized by Ito, 1984) show that the optokinetic reflex is mediated primarily in the mammalian flocculus. Other experiments show that the response is still present in some (e.g. cat) after complete cerebellectomy. The antecedent of the flocculus is the caudal or vestibulo-lateral lobe in fishes while the anterior vermis, which is associated with locomotion and limb movements (Ito, 1984), is related to the corpus of fishes. Thus, localization of the optokinetic response in a small part of the mammalian cerebellum correlates with the limited movements involved. In the same fashion the involvement of most parts of the teleost cerebellum in the optomotor response correlates well with the extensive sensori-motor coordination involved in precise swimming and turning required when following the stripes.

Home-Tank Observations

Whereas the optomotor data did not provide unequivocal evidence of motor involvement, the home-tank observations revealed four postoperative motor disturbances. Three of these, oscillatory movements, wobbling and tilting to the side were relatively mild changes. The fourth, lying on the side, often with the trunk sharply and rigidly curved to one side was clearly a profound motor effect. However, this disappeared in all but one subject in a few hours to a few days, and hence was not present during the optomotor tests. These behavioral abnormalities were very rarely seen in intact fishes.

The short forward and backward oscillatory movements and tilting were observed when the fish were hovering, while the side to side wobbling was only seen when the fish were swimming slowly and only when the fish were undisturbed. It is as if they were unable to remain stationary or maintain an upright position when swimming slowly. Slow swimming is achieved by subtle, highly coordinated movements of the dorsal, pectoral and tail fins (Breder, 1926; Alexander, 1967), by rippling the tail fin and by alternately beating each pectoral fin with a compensatory beat of the dorsal fin. We suggest that ablation of the corpus, total or in part, causes a deficiency in fine motor tasks such as in slow swimming and remaining stationary. Dow and Moruzzi (1958) and Snider (1950) suggest that the overall motor function of the cerebellum is best described as modulation of movements rather than its initiation and control. Moreover oscillatory movements seem to be the counterpart of the well-known mammalian intention tremors.

While all of the cerebellar ablations caused some oscillatory movements, wobbling and tilting, the frequencies differed considerably depending on the type of ablation. Thus, total and large bilateral ablations of the corpus caused the highest levels of oscillatory movements and wobbling, but the highest levels of tilting occurred in the unilateral ablations. This suggests that unilateral deprivations may cause an imbalance in motor function, a subject that has recieved only minimal attention in previous investigations in teleosts (Tuge, 1934; Karamian, 1956). Lying on the side, was hardly ever seen after bilateral corpus lesions, even those involving the entire corpus. Tilting appeared, for the most part, in the unilateral operations of the corpus, especially those also involving the eminentia. This may reflect an imbalance of the vestibular input to the eminentia. Valvula ablation also caused substantial tilting and lying on the side which could relate it to the vestibular system rather than to the corpus as suggested above by the optomotor data. The behavioral changes that we observed after unilateral operations were similar to those described by Tuge (1934) in *Carassius.*

GENERAL

From the optomotor results, the question of motor impairment is less clear. The operated fish continued to swim effectively and they did follow the moving stripes although less efficiently. In contrast to the home-tank observations, there were no apparent differences in optomotor responding between the unilateral and bilateral operates. Lying on side would obviously impair optomotor behavior but this motor defect subsided before the first postoperative optomotor test was given. However, the loss in fine motor control seen in the home tank could account for the loss in efficiency. On the other hand, the optomotor results could also be accounted for by deficits in nonmotor cerebellar functions or in other capacities such as:

A. Decrements in cerebellar arousal. Karamian (1956) noted certain similarities in the functions of the forebrain and cerebellum in fishes particularly with respect to classical conditioning. Aronson and Herberman (1960) and Kaplan and Aronson (1967, 1969) reported similar changes in learning abilities after both forebrain and cerebellar ablations in *Tilapia (Sarotherodon)* which they attributed to decrements in nonspecific arousal or modulatory functions. This could account for the decline in optomotor efficiency in the present study. This hypothesis is supported particularly by our observation that the most striking and consistent change after total or extensive corpus ablation was increased initial latency. The arousal hypothesis also suggests a balancing function for the cerebellum, that is, the cerebellum produces optimal motor output from a variable sensory input.

B. Deficits in the cerebellar learning mechanism. A number of studies have demonstrated deficits in learning (especially classical and instrumental conditioning) after cerebellar lesions in teleosts and in most other vertebrate groups (reviewed by Watson, 1978; McCormick and Thompson, 1984). As noted above, optomotor efficiency improved significantly between the first and last preoperative test. We proposed that the subjects learned to accommodate to the movements of the stripes (Izower and Aronson, 1980). We are now proposing that this preoperative learning was lost abruptly after cerebellar invasion. Furthermore, there was no evidence for relearning in subsequent tests.

C. Difficulty in making abrupt turns. Because of the design of the apparatus the fish tended to swim in a circular path, turn abruptly 180° at regular intervals and resume curvilinear swimming in the opposite direction. It is therefore of considerable interest that swimming speed remained constant (about 600 cm. per min.) in all of the operative groups except VII and IX where extensive unilateral ablations may have caused motor imbalance. In the small rectangular home tanks the fish usually swam in more or less straight lines and made occasional abrupt turns especially when approaching the sides of the aquaria. Here, too, our observations indicated no change in swimming bahavior after the various operations. Apparently the deficits in fine motor control that we discussed earlier did not seriously impair swimming. However, turn latency increased and forward turning frequency decreased. In

> addition, backward swimming and opposite swimming frequencies (i.e. failure to turn) increased. Although the latter measures were not entirely consistent, they indicate that the cerebellar dysfunction affected large and abrupt turning, whereas linear and curvilinear swimming was unaffected.

Swimming behavior of cerebellar-deficient laboratory rats in single and double alternation aquatic T mazes was observed by Pellegrino and Altman (1979). Swimming speed was normal in these subjects but many of the rats showed marked deficiencies in the regular sequential turning required by the pattern of the maze. Similarly in fishes, where regular, sequential turning is an integral feature of our optomotor test, swimming speed was unchanged, but turning was deficient after most cerebellar ablations. Bernton and Torello (1982) cite the Pellegrino and Altman experiment in support of their modulatory conception of cerebellar function in which cerebellar systems are viewed as providing comparable modulatory influences at all major neuraxial and functional levels of sensorimotor and behavioral organization.

A confounding factor in understanding cerebellar function is the remarkable structural variation in different groups of fishes. In some species the body or corpus of the cerebellum is small, and the valvula is tiny (Banarescu, 1957; Khana and Singh, 1966; Schnitzlein and Faucett, 1969). In a great many species, the corpus is of moderate size as is the valvula which is concealed within the optic ventricle. The eminentia granularis are pronounced lateral expansions, but the auricular lobes are often difficult to confirm (Larsell, 1967). In some species the corpus is greatly enlarged and projects forward covering the forebrain, or caudally, covering the medulla. In ostariophysine species the valvula is enlarged and projects dorsally between the two tecta. In the mormyrids the valvula is tremendously hypertrophied and forms a huge differentiated mantle covering completely the rest of the brain. It is obvious that considerable caution is required when extending the functional properties of the cerebellum that we are reporting, to species having markedly different cerebellar configurations.

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