Reversal learning in forebrain ablated and olfactory tract sectioned teleost, *Carassius auratus**

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Groups of goldfish with forebrain ablation and the olfactory tract sectioned were taught a food-motivated nondiscriminative choice in a Y-maze. Criterion choice behavior was followed by successive reversal learning. Both groups successfully acquired each task but the fish with forebrain ablation were slower to eliminate errors in the reversals than were the fish with the olfactory tract sectioned. There were no latency differences between groups on any tasks. It was concluded that the teleost forebrain may, in part, function to provide inhibitory control over previously acquired responses.

Although the pallium, subpallium, nuclei, and related tracts are not highly differentiated, many neuroanatomists (Droogleever-Fortuyn, 1961; Schnitzlein, 1968) consider the primary subdivisions of the teleost forebrain (telencephalon) to be homologous to the limbic areas in higher vertebrates. No gross changes in locomotion, posture, or feeding result from forebrain ablation in the fish (Segaar, 1965). And, while classical conditioning proceeds normally in fish with forebrain ablation (Overmier & Curnow, 1969), instrumental active and passive avoidance are severely disrupted (Hainsworth, Overmier, & Snowden, 1967; Kaplan & Aronson, 1969; Overmier & Flood, 1969; Savage, 1969) and original acquisition in instrumental appetitive tasks is impaired (Savage & Swingland, 1969; Flood & Overmier, 1971).

The effects of forebrain ablation upon successive reversal learning is unclear. Warren (1961) reported that forebrainless fish produce more errors than normals during reversal learning of a positional and brightness cued T-maze task reinforced by food. More recently, however, Ingle (1965) reported that forebrainless fish learned more quickly than normal fish both the initial positional task in a Y-maze and successive reversals when training was not preceded by an alternation task.

Because reversal learning may give us information as to the validity of some hypothesized functions of the forebrain, it is imperative that we explore further the effects of forebrain ablation on the acquisition and successive reversal learning of a

positional task in a Y-maze.

SUBJECTS

Twelve goldfish (*Carassius auratus*) 4-6 in. long overall were assigned unsystematically to two equal experimental groups, forebrain ablated and olfactory tract sectioned. Fish were maintained in single or partitioned aerated aquaria which held dechlorinated tap water. Water temperature was $22^{\circ} \pm 6^{\circ} \text{C}$ over the 6-month experimental period. The fish were fed Gaines Trout Chow (small) every other day in their home tanks prior to the beginning of the experiment. However, once the experiment began, all food was given in the maze and was contingent upon correct responses. During the course of the experiment, two olfactory sectioned and one forebrain ablated fish died of natural causes; data collected on these fish were dropped from the study.

OPERATIONS AND VERIFICATION

The operative procedures have been described in detail by Flood & Overmier (1971). Briefly, Ss were anesthetized in 3% urethane and fixed in sponge clamps. Two dorsal skull bone flaps were made and reflected; then superficial tissue was aspirated, revealing the brain. Both lobes of the telencephalon were aspirated without invasion of the mesencephalon or diencephalon from one group of Ss (forebrainless), while only olfactory tracts were severed just rostral to the telencephalon (bulbs left intact) in the other group (olfactory); no brain tissue was damaged in this second group. The bone flaps were then replaced and fastened in place with surgical thread. Five days were allowed for recovery.

At the end of the experiment, Ss were sacrificed and their heads fixed in 7% formalin, after which the brains were removed for gross inspection and photographing. Figure 1 shows a composite drawing from enlarged photographs of the average extent of

tissue destruction relative to a normal brain. There was little variation among ablations.

APPARATUS

The apparatus was a black acrylic Y-maze with three equal arms 10 in. long, 4 in. deep, with water depth of 3 in., and $3\frac{1}{4}$ in. wide. The arms were at a 120-deg angle to each other. Three yellow acrylic gates were placed 7 in. from the end of each arm and were attached to a bar such that they were all raised and lowered simultaneously. The start arm had a 40-W lamp which could shine through a translucent end panel acting as a trial start SD. An electric timer measured latencies of choice responses (gate up to gate down).

PROCEDURE

Following recovery, the Ss received experimental treatment every other day. They were 48 h deprived at the onset of each session. Treatments began with adaptation (all gates up) until the fish freely ate on two consecutive sessions. Then maze training began; fish received 10 trials per day with an intertrial interval of approximately 1 min. A S was placed in the startbox facing the gate; 30 sec later the SD was turned on, and the gate was raised. The "choice" criterion for trial termination was entering an arm to the extent that the fish's operculum was beyond the gate. If a maximum 30 sec latency was exceeded, the fish was forced to make a choice and the trial terminated. The correct, or reinforced, side arm of the maze for original acquisition was determined randomly for each fish. Swimming into the correct arm was immediately reinforced with 2-3 grains of food. Fish remained in the chosen arm for 30 sec and then were returned to the startbox. The acquisition criterion was three consecutive sessions with at least 90% correct choices on each. Upon attainment of criterion, the "correct" arm was reversed so that the previously positive arm was no longer reinforced and the

Fig. 1. Extent of forebrain ablations relative to a normal brain. Drawing based upon photographic projections. Scale: 2.5 times actual size. (1. Forebrain; 2. optic lobes; 3. cerebellum; 4. valgal lobes; 5. spinal column.)

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Fig. 2. Mean daily percentages of correct responses by each group.

previously negative arm was reinforced. The learning criterion for each reversal was the same as for original acquisition. The original acquisition was called Task 1, the first reversal was called Task 2, etc. There were a total of four tasks.

Because taste or some other chemosensory gradient might exist in the maze water, the water from the different maze segments was mixed by means of a commercial baster between each trial. In addition, a small cotton bag of Trout Chow was hung in each goal arm.

RESULTS

The individual daily mean percentages correct for each task are presented in Fig. 2 and were subjected to a three-way analysis of variance (ANOVA) with repeated measures. Just the first 6 days of each task were included because some Ss had satisfied the acquisition criterion by that time on some tasks. It is clear that both the olfactory group and the forebrainless group learned each task (days, $F = 21.61$, $df = 5/35$, $p < .001$; Groups by Days, F n.s.; Groups by Days by Tasks, F n.s.). However, the groups differed in their ability to learn the tasks; the forebrainless group was markedly inferior to the olfactory control group (Groups, $F = 11.21$, $df = 1/7$, $p < .01$) and was inferior on all reversals (Groups by Tasks, F n.s.). There is also a noticeable trend for successive reversals to become more difficult for both groups (tasks, $F = 6.98$, $df = 3/21$, $p < .01$).

The difference between the groups on successive reversals appears early in that forebrainless fish tend to persist in the previously learned behavior longer than the olfactory fish. This is confirmed by an ANOVA of the

number of days to reach 50% correct (i.e., nondifferential responding). The olfactory group reached the 50% correct point sooner than did the forebrainless group (Groups, $F = 10.96$, $df = 1/6$, $p < .05$).

Mean daily response latencies for the first 6 days of each task are presented in Fig. 3. Analysis of latencies revealed that the two groups did not differ in the individual mean latencies on each task (groups, F n.s.; Groups by Tasks, F n.s.). Despite this failure to find evidence for a difference, the apparent difference between groups on Task 1 prompted an analysis of the individual daily mean latencies for that task alone.

Fig. 3. Mean daily latencies of choice responses by each group. Maximum latency was 30 sec.

This second analysis confirmed the first in that there was not even a borderline significant difference between the groups (groups, $F = 3.32$, $df = 1/7$, $p > .10$).

DISCUSSION

The present experiment generally confirms the earlier report by Warren (1961), that forebrainless fish compared to normal fish are impaired in their learning of successive reversals. Our experiment differed in that it controlled for possible olfactory factors and for the effects of loss of olfaction by using as controls fish which had their olfactory tracts sectioned. We are at a loss to explain Ingle's (1965) report of facilitated reversal learning except to attribute the difference to the unique reinforcement he employed—avoidance of glass barriers.

Despite the observed impairment in forebrainless fish, the forebrainless fish did nonetheless eventually learn each task to the same asymptote as the olfactory controls. This is consistent with the Flood & Overmier (1971) report, that while ablation slows learning of runway tasks, the forebrainless fish do eventually learn to the same asymptote.

The general learning deficits evident in forebrainless fish have been attributed to a variety of functional disorders such as loss of arousal (Aronson, 1957), loss of ability to inhibit responses (Segaar, 1965), and others. If the forebrain plays a role in the inhibition of ongoing behaviors, then one would expect forebrain ablation to produce a deficit in reversal learning that was manifest early in each reversal as persistence in

the previously reinforced response. That is exactly what was observed in the present experiment. Thus, the present results are consistent with the hypothesis that the forebrain is a source of inhibitory control.

A test of the hypothesis that removal of the teleost forebrain produces a deficit in arousal is also possible in the present experiment. If there is an arousal deficit in forebrainless fish, then the response latencies of the forebrainless fish should always be slower than those of the control Ss. The results of this experiment reveal that no such difference exists; even the hint of a difference in Task 1 proved to be ephemeral. The present results, therefore, are not consistent with the arousal hypothesis.

In summary, it appears that while the teleost forebrain is not essential to the learning of complex appetitively motivated tasks, the forebrain does facilitate such learning. This facilitation does not seem to be by means of nonspecific arousal of lower brain centers in control of complex

behaviors but by means of (at least in part) providing inhibitory control over previously acquired responses.

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