XVIII. CUTANEOUS SENSORY MECHANISMS[*]

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A. NEUROPSYCHOLOGICAL EFFECTS OF EARLY SENSORY RESTRICTION

1. Introduction

We have previously reported[1] that dogs raised in restriction cages from puppyhood to maturity have greater difficulty than normally reared littermates in performing a simple black-white discrimination and in subsequent reversal training. Since the restricted dogs had some patterned visual stimulation in their cages, their difficulty in performing a discrimination and then utilizing it in a new situation could not be attributed to a deficit in pattern perception. Rather, the explanation seemed to lie in the exceptionally high level of emotional excitement that pervades all of the behavior of restriction-reared dogs, including "whirling fits" that resemble a seizure.[2]

A possible hypothesis to account for almost all of the behavior of restriction-reared animals is that they are so "aroused" and distracted by the unfamiliar environment surrounding them that they have difficulty in attending selectively to the "cue" properties of the stimuli to be discriminated. The effects of restriction thus seem best explained in terms of a cue/arousal (signal/noise) model,[3] which suggests that high levels of arousal interfere with discrimination and differentiation of relevant cues from the total environmental input. The nature of the deficit in restriction-reared dogs, then, appears to be difficulty in selection of relevant cues and inhibition of irrelevant inputs at low synaptic levels of the central nervous system.

2. Current Activities

Two kinds of experiments are now being carried out: (a) behavioral experiments aimed at elucidating the nature of the abnormalities exhibited by dogs reared in perceptually restricting cages, and (b) studies of the EEG, as well as electrical responses evoked at the cortex by visual stimulation, in an attempt to discover some of the neural mechanisms that might account for the inadequate differentiation of relevant and irrelevant sensory inputs.

Comparison of restriction-reared and normally reared littermates in a series of behavioral tests provides evidence suggesting that the restricted dogs have greater difficulty than the control dogs in inhibiting irrelevant responses (responses that once were instrumental in bringing them food rewards). Moreover, they are also unable to differentiate adequately among auditory stimuli, or to respond adaptively to stimuli

that have sexual relevance.

Preliminary electrophysiological studies carried out in collaboration with Professor Rosenblith and Mr. Stephen K. Burns thus far have provided evidence that is suggestive (but not conclusive) that the patterns of cortical responses evoked by light flashes differ in the two groups of dogs. The preliminary evidence has led to our present program of research in an attempt to discover differences in neurophysiological activity between restricted and normally reared dogs.

3. Failure in Extinction of Irrelevant Responses

Observations made during earlier experiments on visual discrimination and reversal learning[1] suggested that the restricted dogs had difficulty in inhibiting or "holding back" incorrect responses. Once they started running toward a particular side in the discrimination box, they would veer toward the correct stimulus but were not able to stop themselves in time to keep from hitting the door carrying the incorrect stimulus card. The restricted dogs usually developed a position habit that they seemed to be unable to break even at the late stages of the learning process. The dominance of such position habits (running at least 9 out of 10 trials to the same side of the apparatus) is greater in restricted than in normally reared dogs. The restricted dogs exhibited a position habit on 64 per cent of the test days, while normal dogs had a position habit on only 16 per cent of test days. The difference is significant at the 5 per cent level ($\chi^2 = 6.08$).

An experiment was therefore undertaken to test the hypothesis that restricted dogs will have greater difficulty than the control dogs in inhibiting irrelevant responses. If they are taught to make a simple response to obtain food (pressing a window in a specially constructed cage) and then food is later withheld, the hypothesis suggests that the restricted dogs will continue to press the window for longer periods of time than the control dogs.

The subjects of the experiment were two restricted dogs (Dulla and Sin) and three normally reared littermates. The five dogs were placed daily in a large cage that had two windows and their behavior was shaped so that each press on either window triggered an apparatus that dropped a food reward (a piece of frankfurter) into the cage. Each press produced a click, a fairly loud buzz from a door buzzer in the electric circuit, and a "ping" when the food landed in the cage. Both groups of dogs learned the response relatively quickly, and there was no difference between the two groups in the number of rewards necessary to "shape" satisfactory pressing behavior. The dogs were then given twelve 10-minute periods (one period per day) to achieve a stable response output.

Although there were no differences between the results for the two groups in mean pressing rates, their behavior differed markedly. Dulla developed the curious habit of turning two complete circles before pressing the window and obtaining food. The level
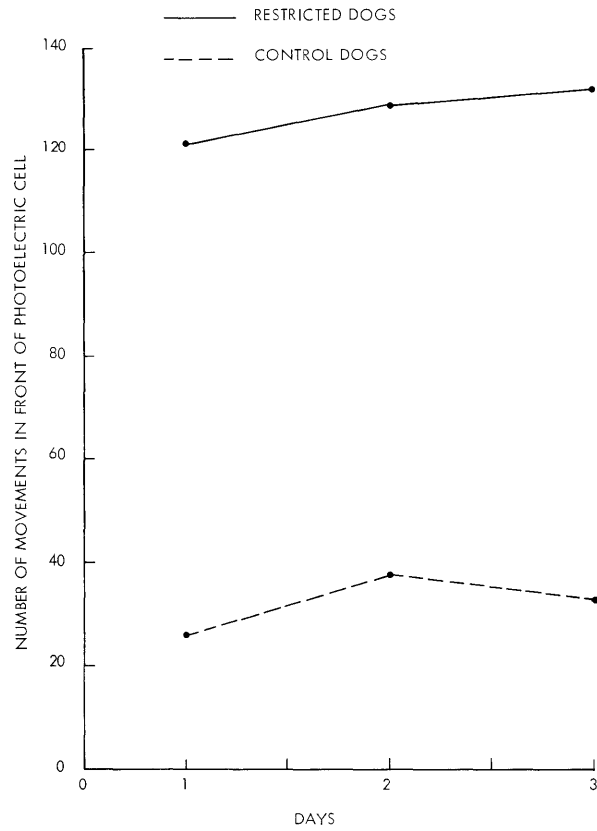
Fig. XVIII-1. Activity levels of **restricted** and **control** dogs during 5-min periods on **three** successive test days.
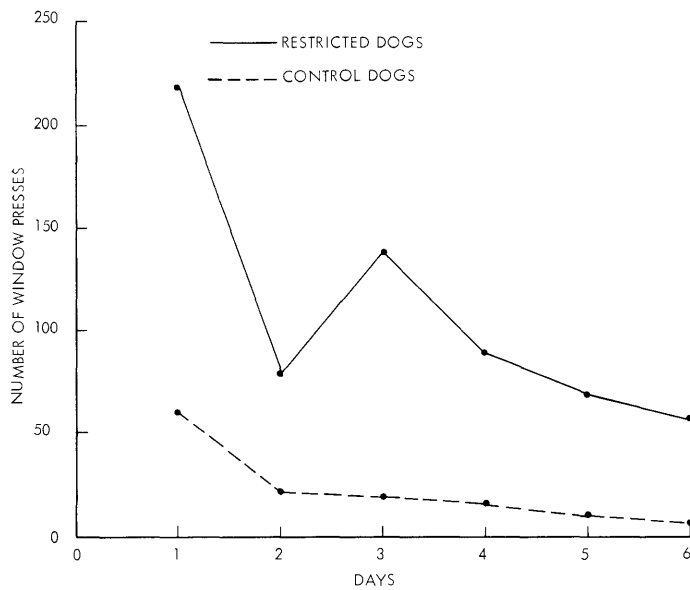

Fig. XVIII-2. Number of window presses made by restricted and control dogs during six extinction periods.

of his activity in the cage was astonishingly high. Measures of activity obtained by an electrically triggered counter that recorded the number of times the dogs moved in front of a photoelectric cell in the center of the cage are graphically presented in Fig. XVIII-1.

Sin also showed a high level of excited activity in the test box, but she developed an entirely different behavior pattern. As soon as the first food reward landed in the cage, she licked the slice of meat, rolled it around the cage, rubbed her head against it, and finally left it in a corner. She then pressed again and repeated the same pattern until she collected a small pile of rewards (one to two dozen) and then ate them voraciously (sometimes promptly regurgitating them and re-eating them). She thereafter pressed like a normal dog for the remainder of the test period. Behavior patterns like those of Sin and Dulla were never observed in any of the normal dogs.

Once a stable response output was achieved, the dogs were given six 20-minute extinction periods in the test cage (one period per day) in which their presses were no longer rewarded. They were usually fed 4 to 6 hours after the test session so that feeding would not be temporally associated with activity in the box.

Figure XVIII-2 shows the extinction rates for the two groups of dogs. It is clear that the restricted dogs showed a significantly higher rate of pressing during extinction (p = 0.01; Fisher direct probability test), even though the earlier, rewarded pressing rates for the two groups are not statistically different. This experiment provides evidence that the restricted dogs fail to inhibit irrelevant responses. But the reason for this failure is not clear. It may be due to an inability to stop or inhibit a response tendency (purely on the motor side) or it may be due to a failure to perceive the absence of clicks, buzzes, and pings that once signalled arrival of food. Their difficulty in differentiating auditory stimuli is clear from other experiments reported here. Possibly, these stimuli even failed to play a relevant role in the initial response acquisition. The absence of reinforcement alone, however, is not enough to produce extinction of the pressing response.

4. Failure in Discrimination of Sexually Relevant Cues

During the tests on instrumental feeding responses (pressing behavior), one of the female dogs in the colony (not used as a subject in the current tests) came into heat. The behavior of the two male control dogs was strikingly different from that of the restricted male. When each control male dog was allowed access to the female, his behavior was goal-directed and the goal was unmistakable. Each began courting behavior, followed by mounting and intromission. When not in the presence of the female, each whined, jumped excitedly about, ignored the food in the apparatus, and spent the 10-minute test period trying to leap out of the cage.

The male restricted dog, however, ignored the presence of the female and continually avoided her approaches. Although the presence of the female appeared to evoke
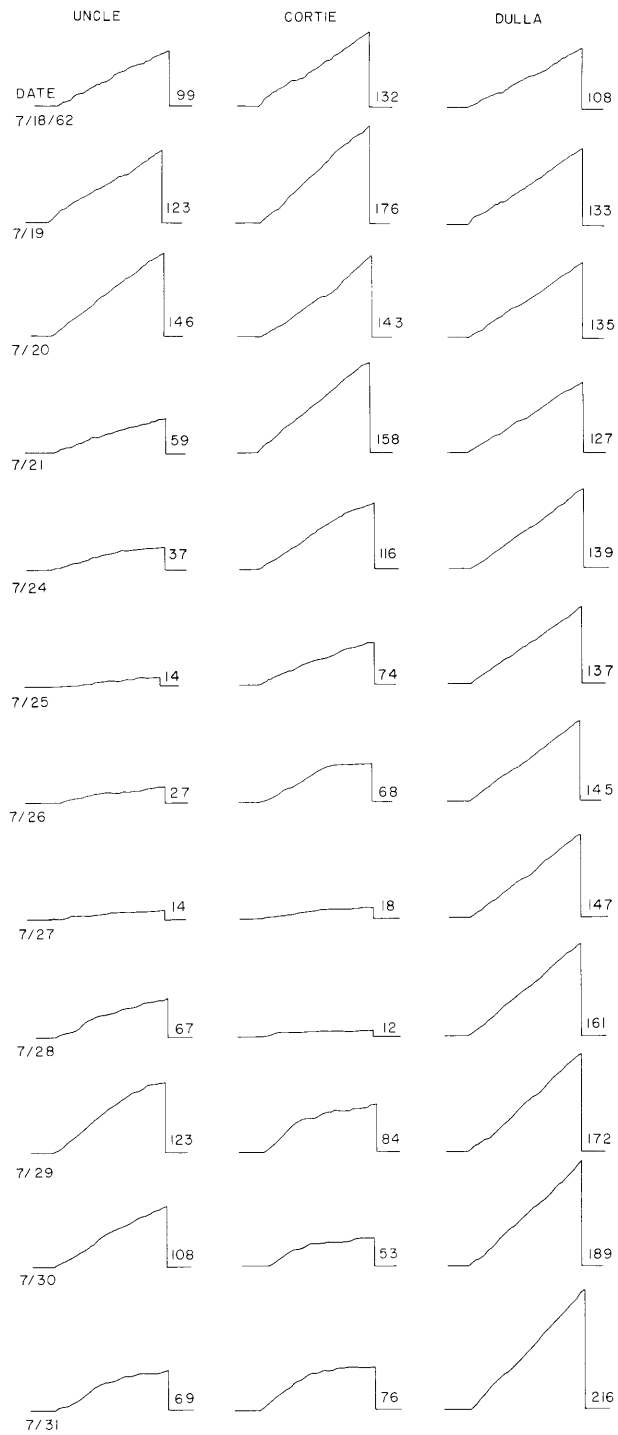
Fig. XVIII-3. Effects of sexually relevant stimuli on window-pressing rates by one restricted (Dulla) and two control (Uncle, Cortie) dogs.

a generalized excitement, it failed to produce any goal-directed behavior. Moreover, the behavior of this dog (Dulla) in the testing cage was totally unlike that of the control dogs: his rate of pressing for food increased day by day, in sharp contrast to the disinterest in food exhibited by the control dogs. None of the females showed either a rise or decrease in pressing that was related to the activities of the female in heat.

Figure XVIII-3 shows the cumulative window presses made during the 12-day period when each dog was placed in the cage for 10 minutes a day. The increased pressing rate of Dulla and the sharp drop in pressing by the control dogs at times of maximal interest in the female are clearly seen. The graphs also reflect the fact that Uncle's interest in the female was aroused before Cortie's. Cortie showed maximal interest only after Uncle consummated his courtship. No rivalry between the two was manifest at any time; rather they achieved their goal seriatim. It is evident, then, that olfactory and other related stimuli that had particular relevance for the control dogs served only to increase the general state of activity of the restricted dog — that is, produced a general arousing effect rather than specific cue-oriented, goal-directed behavior.

5. Differential Behavioral Effects of Auditory Stimuli

A series of tests was carried out to study the effects of auditory stimuli on the behavior of the two groups of dogs. The window-pressing procedure to obtain food was again used to provide a stable behavioral response that would reflect the effects of presentation of auditory stimuli. Three tests were carried out.

(a) After the final extinction period (the sixth extinction day), the dogs were placed in the test box for a 15-minute period in which activity and pressing (without reward) were recorded. Two minutes after the dog was placed in the box, a 15-second tape recording of a lion roar was presented through a loud-speaker standing above the windows of the test box. The same recording was subsequently played every two minutes thereafter until the end of the 15-minute period. The effect of the lion roars was to diminish the number of responses in both groups. The magnitude of the response decrease, however, was different: the window-pressing output of the control group decreased 86.8 per cent; none of the normal dogs even approached the window after the first lion roar. The restricted dogs, on the other hand, became intensely excited, and one of them had a "whirling fit."[2] They resumed pressing, however, so that the over-all decrease was 47.3 per cent. The difference between the two groups is significant at the 5 per cent level (t = 3.03; one-tail test).

(b) On three successive days the dogs were given a 10-minute period in the test box each day, in which they received a food reward each time they pressed the window. No sounds were presented the first day, but on the second and third days the 15-second tape recording of lion roars was presented every two minutes. Since one of the restricted dogs (Sin) sometimes regurgitated her food after 5 minutes of pressing, as we have
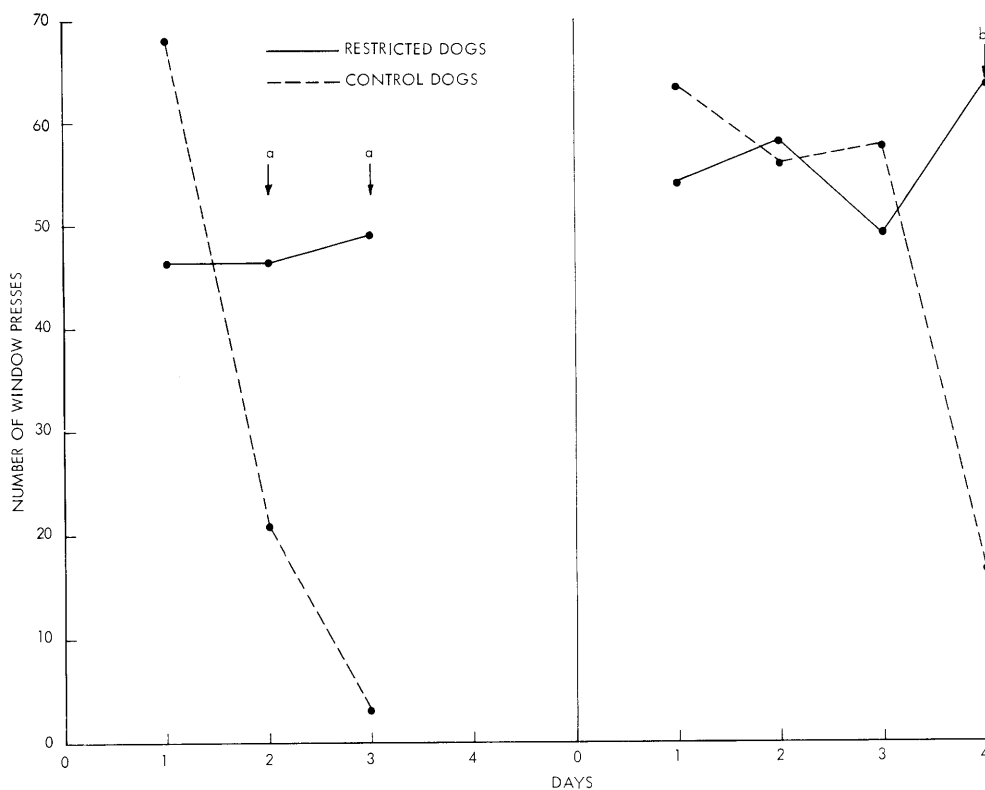
Fig. XVIII-4. Effects of presentation of auditory stimuli
(indicated by arrows) on window-pressing
behavior. (a) Lion roars. (b) Cock crows.

pointed out, the two groups are compared for their response output for the first 5-minute periods. The results are shown in Fig. XVIII-4a. It is clear that the control dogs showed marked decreases in their window-pressing output, while the restricted dogs showed no significant change.

(c) On four successive days the dogs pressed the window to obtain a food reward. On the fourth day a 15-second tape recording of a cock crowing was presented every two minutes. Figure XVIII-4b shows the effects of the auditory stimulus on the response output by each group during daily 5-minute periods. While the control dogs pressed fewer times during the period of auditory stimulation, the restricted dogs increased their response output.

The results of these tests show that auditory stimuli produce different effects in the two groups of dogs. Sounds of lion roars and cock crows tend to produce marked disruption of spontaneous or rewarded window-pressing behavior of normal dogs, while they tend (after a small number of presentations) to raise the general response level of the restricted dogs. The percentage changes in pressing output (compared with the output of the period before auditory stimulation) is graphically presented in Fig. XVIII-5.
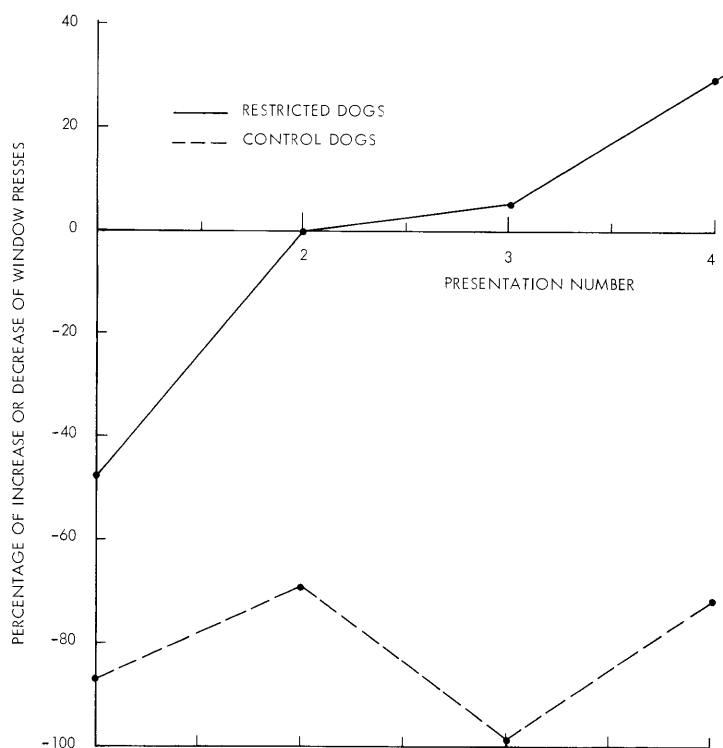
Fig. XVIII-5. Percentage of increase or decrease in window-pressing behavior produced by four presentations of auditory stimuli. 1, 2, 3: lion roars. 4: cock crows.

The difference between the two groups is significant at the 1 per cent level ($\chi^2 = 6.94$).

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B. TAIL-FLIP REFLEX IN GOLDFISH

A behavioral study was carried out by Willard L. Rodgers (Senior Thesis student in biology) in collaboration with Dr. John R. Segal, of the Boston Veterans Administration Hospital, and the writer, on the tail-flip reflex in goldfish. The "tail flip" consists of a sudden flexion of the fish's tail to one side or the other, with the result that the fish

lurches forward. The "flip" may occur in response to a variety of stimuli but is evoked most consistently by pressure waves produced by taps on the side of the aquarium.

The tail flip is of particular interest, since there is reason to believe that it is produced by the activity of two giant nerve cells known as the Mauthner cells. Segal[1] has obtained physiological evidence of complex sensory interactions occurring at these cells. His studies show that stimulation of the eighth nerve on one side of the body is capable of inhibiting activity produced by stimulation of the eighth nerve on the opposite side. (The eighth nerve is normally stimulated by pressure waves in the water.) He also obtained evidence of a habituation effect, in that the ratio of electrical responses to stimulation of the eighth nerve is decreased with increasing number of presentations. Moreover, he obtained evidence of a visual input to the Mauthner cell, even though visual
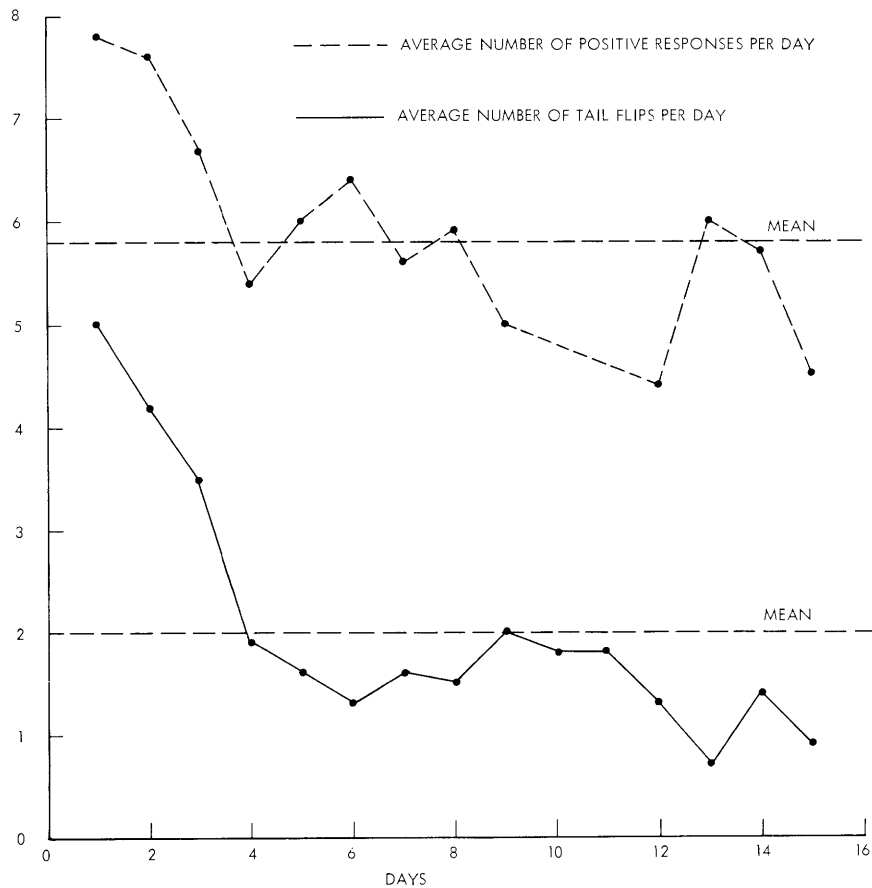

Fig. XVIII-6. Habituation of the tail-flip response and the total number of positive responses. Ten fish were each given 10 taps per day, while below the surface of the water, for 15 days. The lower graph indicates the average number of tail flips shown by the 10 fish on each day. The upper graph indicates the average number of positive responses (tail flips plus any other movements) shown by the 10 fish on each day.

stimuli are generally ineffective in producing a tail flip.

That such complex sensory interactions can occur at the site of a single cell, which can be studied relatively easily because of its large size, has made the Mauthner cell the subject of a series of recent physiological studies. No comparable psychological studies have been made, however, in the attempt to link physiological activity with behavior.

Our behavioral experiments have provided evidence that parallels the physiological observations. Two major points of interest emerged from the study.

1. Habituation of the Tail-Flip Reflex

We found that the frequency of the tail-flip reflex decreased with successive presentations of the stimuli (constant-energy taps on the wall of the aquarium). Figure XVIII-6 shows that the drop in response frequency occurred over a period of days. The 12 fish in this experiment gave an average of 5.0 tail flips per 10 stimuli on the first day, and the frequency dropped rapidly during the first 4 days. On the fourth through the eleventh days, there is a plateau in the frequency of tail flips. It is interesting to note, however, that the average number of positive responses to the taps, such as turning and reorienting the body and moving the fins, does not decrease in frequency to the same extent as the tail flips (see Fig. XVIII-6).

2. Interaction of Visual and Eighth Nerve Inputs

a. Procedure

Three groups of fish, comprising a total of 22 fish, were used in this experiment.

Group I: Six fish were given 10 visual stimuli (a dark blue sheet of paper moved across the top of the experimental tank) and 10 taps on the first and second days, and again on the thirteenth day. On these days the taps and visual stimuli were administered separately but during the same experimental session. On the third through the twelfth days, these 6 fish were given 10 taps and visual stimuli simultaneously, by administering the tap while the sheet was being moved across the top of the tank.

Group II: Ten fish were given 10 taps for 15 days.

Group III: Six fish were given 10 taps alone for 10 days. On the eleventh and twelfth days, these six were given simultaneous taps and visual stimuli.

b. Results

The results are summarized in Fig. XVIII-7. In the first place, it is apparent that the visual stimulus alone is almost totally ineffective in eliciting the tail-flip response under the given experimental conditions. However, if the visual stimulus is administered simultaneously with the tap, the frequency of tail-flip responses is raised significantly above the frequency of responses to taps alone; this is shown by the large
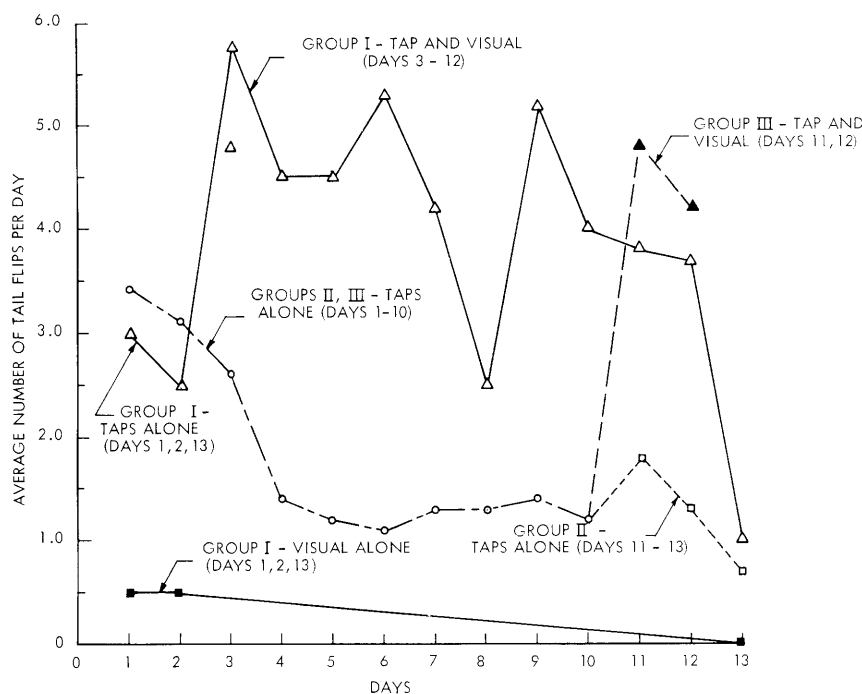
Fig. XVIII-7. Interaction of stimuli. The six fish in Group I were given ten
taps and ten visual stimuli (separate) on days 1, 2, and 13, and
ten simultaneous taps and visual stimuli on days 3-12. The ten
fish in Group II were given ten taps on days 1-13. The six fish
in Group III were given ten taps on days 1-10, and ten simul-
taneous taps and visual stimuli on days 11 and 12.

increase in frequency of tail flips exhibited by fish in Group I on the third day, when the
two stimuli were presented simultaneously, as compared with the slight decrease in
frequency on the third day exhibited by fish in Groups II and III, to which taps alone were
still being given. Further evidence of the interaction of the stimuli is provided by the
increase in frequency of tail-flip responses exhibited by fish in Group III on the eleventh
and twelfth days, when this group was given the simultaneous stimuli, and again by the
drop in frequency exhibited by fish in Group I on the thirteenth day, when the stimuli
were again presented separately.

A more detailed comparison of the frequencies confirms the effectiveness of the
simultaneous stimuli in producing the tail-flip response. Fish in Group I gave an aver-
age of 2.5 tail flips per fish per day on days 1, 2, and 13 (separate stimuli) to both vis-
ual stimuli and taps (that is, 2.5 responses per 20 stimuli) compared with an average
of 4.4 tail flips per fish per day on days 3 to 12 to the 10 combination stimuli. Group III
gave an average of 0.7 tail flips per fish per day on days 1-10 to 10 taps per day, com-
pared with an average of 4.5 tail flips per fish per day on days 11 and 12 to 10 combi-
nation stimuli.

By combining the data on days 1, 2, and 13 for Group I, days 1-12 for Group II, and days 1-10 for Group III, the over-all average for the number of tail flips in response to 10 taps is 1.8 tail flips per fish per day. This may be compared with the combined data for days 3-12 of Group I and days 11 and 12 of Group III, which give an over-all average for responses to 10 combined stimuli of 4.4 tail flips per fish per day. Thus the frequency more than doubled if the visual stimulus was presented simultaneously with the tap.

3. Conclusions

If the tail flip is a simple reflex meditated by the Mauthner cells, an explanation must be sought for the failure of the fish to display this response to every stimulus presentation. Segal's[1] observation that stimulation of the contralateral eighth nerve results in inhibition of the response of the Mauthner cell to stimulation of the homolateral eighth nerve indicates that inhibitory phenomena do indeed occur. But the phenomena of habituation of the tail flip over long periods of time, together with the increase in tail-flip responses when visual stimuli are presented simultaneously with the taps, suggest far more complex mechanisms. Whether this "learning-not-to-respond" is the result of changes in physiological conditions at the site of the Mauthner cells or is brought about by inputs to the cells from other brain areas may be answered in future physiological studies.

It is noteworthy, however, that the total positive responses decreased less markedly on successive days of testing compared with the rather rapid habituation of the tail-flip response. This continuation of positive response may be comparable to the observation[2] that ducks continue to give a high frequency of orienting responses to "hawk" and "goose" shapes moving overhead long after they cease to show fear responses. Thus the fish may continue to take note of the stimulus, but in the absence of other information not actually try to leave the area.

It is clear that the simultaneous presentation of pressure wave and visual stimuli results in a significantly higher frequency of responses than do either of the stimuli when presented separately. It is known that there are afferents to the Mauthner cells from the optic tectum, as well as from the eighth nerve.[3] The results indicate, however, that both types of afferents have different effects. Pressure waves are able to evoke the tail flip reliably (before habituation has occurred), while visual inputs from the optic tectum cannot. It is possible that the difference may be attributed simply to the number of fibers innervating the Mauthner cells. The eighth nerve may have a sufficiently large number of fibers going to the Mauthner cells to produce an action potential. The fibers from the optic tectum may only produce depolarization, and thus facilitation, but may not be sufficient to trigger an action potential.

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References

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