Feeding Behavior and Electrical Stimulation of the Brain of Carassius auratus

Abstract. Bipolar electrodes were implanted in large goldfish in olfactory and nonolfactory areas of the central nervous system. Stimulation of olfactory areas elicited stereotyped feeding activity indistinguishable from normally induced behavior. It is suggested that the olfactory rather than the peripheral gustatory system plays the predominant role in the arousal of feeding activity.

In the investigations under discussion it has been possible to observe the behavior of goldfish after electrical stimulation to various areas of the brain. The study emphasized investigation of normal feeding patterns and comparison with feeding behavior in fish with implanted electrodes living in the same environment. The first part of the study dealt with the observation and description of normal behavior. Ethologists such as Lorenz (*1*) have correctly pointed out that before a casual role can be assigned to a particular act, the complete range and variation of behavior seen in the species must be known. The goldfish used in this study were 15 cm or more long. Goldfish of smaller size exhibit additional patterns of feeding but are not discussed here. The endogenous feeding maneuvers seen in the larger fish were used as a reference, and changes in this behavior during and after brain stimulation were studied.

Large goldfish feed in a characteristic way. The entire pattern, from an appetitive phase of arousal and search to the consummatory conclusion of swallowing materials, can be described in both laboratory and free-living forms. Under laboratory conditions of food deprivation, hungry fish, when encountering a familiar food odor (*2*), will demonstrate a complete feeding pattern—for example, immediate arousal and wandering, followed by a phase in which objects on the aquarium floor are selectively attacked. A non-object-seeking phase continues, with the fish canting head-to-sand, indiscriminately sampling large areas of sand for food. This activity generally signals the end of a feeding performance.

Goldfish possess an external system of taste buds, variously extending over the snout and anterior structures of the body (*3*). Since a food odor placed in the aquarium was capable of eliciting feeding behavior in the hungry fish, the experiment described below was carried out to ascertain whether the peripheral gustatory or the olfactory system played the major role in initiating feeding activity.

Two goldfish were reinforced to perform endogenous feeding patterns in the presence of a food odor. At the end of the training period, both fish, within a few seconds of encountering the odor, would exhibit typical arousal with bottom-feeding maneuvers. They exhibited this activity with absolute regularity, in isolation or together. The anterior portal of the olfactory pits of one fish was gently occluded with cotton pledgets. This temporarily prevented access of odor to the pit organ; the peripheral-skin taste system remained undisturbed. When the odor test was repeated, the control fish responded with a feeding performance; the other fish showed no response. This experiment could be repeated, either fish serving as control. From these observations, it was concluded that an olfactory cue triggered feeding activity in hungry fish.

A second phase in the study of feeding behavior involved chronic implantation of bipolar electrodes in olfactory and nonolfactory areas of the brain. Stimulation of the olfactory crura, extending from olfactory bulb to forebrain, initiated the complete feeding performance described for control fish, and this corroborated the observations on olfactory occlusion.

Table 1 summarizes data from investigations on 15 fish with electrode implantations. The average number of sessions for each fish in the experimental situation was four. Each session, which included several experiments at different implantation sites, lasted between 2 and 4 hours. Feeding performance was evaluated in terms of intensity and completeness of response. Intensity was a measure of the motor components characterizing the response; completeness was measured by comparison with control fish under conditions of food deprivation.

Stimulation of olfactory crura produced complete feeding responses in nine of 13 fish, with the arousal, intention movements, and low-intensity feeding commonly seen in other experiments. The stimulus parameters were 0.075- to 0.15-ma pulses of 0.5-msec duration, in pulse trains of 10 to 25 seconds at regular intervals of 1 to 3 minutes. Frequencies of 30 to 50 pulses per second gave the best feeding responses. Higher frequencies were ineffective. Adrian and Ludwig (*4*), using decapitated specimens of carp and goldfish, reported normal discharges of 40 per second from the olfactory bulb after the flushing of odoriferous food materials across the olfactory organ. This agrees with our data on the frequency of stimulus used in central arousal of feeding in goldfish.

The forebrain areas stimulated encompassed the lateral and medial olfactory regions of secondary synapse and the anterior aspects of piriform and hippocampal elements. In only one of 15 implants was a complete and intense pattern seen after forebrain stimulation. Generally, when forebrain responses occurred, they were often preceded by experiments in which crural feeding responses were seen. Responses from this area were characteristically incomplete and of low intensity, coming in single rather than continuous displays. Lower current ranges of 20 to 60 μa were effective.

Stimulation of vagal lobes produced no preliminary feeding arousal. Feeding maneuvers observed in response to stimulation were also preceded by successful crural responses. The movements were sudden and incomplete, and came as solitary events during the course of an experiment. Stimulus parameters were similar to those in forebrain studies. Other areas stimulated showed no feeding responses (*5*).

Table 1. Data on electrical stimulation of the brain and on feeding behavior in *Carassius auratus*.

Area of stimulation	Fish	No. of expts.	Nonfeeding motor responses	Feeding		Complete feeding performance	
				Arousal	Intention movements	Low intensity	High intensity
Crura	13	44	13	12	7	1	11
Forebrain	15	50	26	4	6 (4)*	11 (6)*	3†
Vagal lobe	5	10	2	0	4 (3)*	4 (3)*	0
Facial lobe	4	6	6	0	0	0	0
Valvula	5	9	9	0	0	0	0
Cerebellum	2	3	3	0	0	0	0

* Stimulation of olfactory crura preceded this experiment by several minutes or more. Numbers in parentheses represent successful crural feeding responses. † Data recorded from the same fish.

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References and Notes

1. K. Lorenz, *Symposia Soc. Exptl. Biol. No. 4* (1950), p. 221.
2. The food odor was that of a rodent pellet extract (Staley's Rockland rabbit ration).
3. C. J. Herrick, *J. Comp. Neurol.* **15**, 375 (1905).
4. E. D. Adrian and C. Ludwig, *J. Physiol. (London)* **94**, 441 (1938).

5. This report is adapted from a thesis submitted in partial fulfillment of the requirements for an M.S. degree in physiology. This work was supported by a U.S. Public Health Service postsophomore medical school fellowship (PX-117-3) and by grants to R. W. Doty from the Foundation Fund for Research in Psychiatry and from the National Institute of Neurological Diseases and Blindness (B-1068).

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Inhibition of Central Auditory Response

Abstract. Suitable electrical stimulation of the region of the decussation of the olivocochlear bundles, which supply efferent innervation to the organ of Corti, was found to abolish the response of the auditory cortex to a click, without changing the responses (N_1 and N_2) of the eighth nerve in cats. At higher stimulation values the eighth nerve responses also were abolished, and at intermediate stimulus values responses at the medial geniculate and inferior colliculus were suppressed.

Inhibitory pathways of the nervous system have been much studied in recent years. In the auditory field, Rasmussen (*1*) found efferent fibers (the olivocochlear bundle) to the peripheral organ, and Galambos (*2*) reported that under certain conditions stimulation of these efferent fibers markedly reduces the N_1 and N_2 components of the changes in electrical potential that occur at the round window membrane when the ear is exposed to sound. Desmedt (*3*) located, in the posterior lateral part of the diencephalon, an area the stimulation of which decreased the potentials evoked in the cochlear nuclei. The experiments that are reported here demonstrate a further effect of stimulating the region of the olivocochlear bundle.

Thirty-four adult cats were anesthetized with Nembutal (25 mg/kg) and maintained at a light level of sedation. One animal, in addition to Nembutal, after the insertion of an endotracheal tube, was given a constant infusion of a neuromuscular blocking agent, Flaxidle, and maintained on artificial respiration. The level of the Flaxidle was such that no movement could be elicited by any means of stimulation. Potentials were recorded from the auditory cortex with a monopolar silver ball electrode, from the medial geniculate and inferior colliculus with bipolar stainless steel electrodes, and from the round window with a silver foil electrode. A stainless steel bipolar electrode with an outside diameter of not more than 2 mm was used to stimulate the region of the olivocochlear bundle. A pair of Tektronix type 122 preamplifiers and cathode ray oscilloscope were used to amplify the responses. Auditory stimuli consisted of a 0.075-msec click delivered by a crystal microphone connected to a hollow ear bar. Electrical shocks to the region of the olivocochlear bundle were generated by a Grass stimulator through a stimulus isolation unit. They were of 1 msec duration, at a repetition rate of 100/sec, and were on for a total duration of 320 msec. In all of the experiments there was a 5-msec delay between the end of the electrical stimulation and the onset of the click. At the end of each experiment the animal was sacrificed with all of the electrodes in place, and perfused with normal saline and then with 10-percent neutral formalin. All of the brains were saved for histologic examination.

A small region, 10 mm rostral from the obex on the floor of the fourth ventricle, was found which, upon stimulation, would inhibit the eighth nerve response, the N_1 and N_2 of the round window response. This confirmed the previous work of Galambos (*2*). When stimuli to the region of the olivocochlear bundle which were not strong enough to inhibit the N_1 and N_2 were used, the cortical-evoked potential to a click was markedly suppressed or abolished (Fig. 1). Cortical suppression was accompanied in some animals by a slight reduction in the eighth nerve response and in others by no change at all in the eighth nerve response. These observations have been repeated in 34 animals. The response at the medial geniculate to a click was suppressed by shocks to the region of the olivocochlear bundle. These shocks were also accompanied by some reduction but not total suppression of the eighth nerve response. The same relationship was found for the inferior colliculus, in that it could be suppressed, but only after the N_1 and N_2 were somewhat diminished. The inferior colliculus in some animals was never totally suppressed until the eighth nerve response was abolished.

In all of the experiments the region which gave the maximal central inhibition was identical with that which gave the maximal suppression of the eighth nerve response. Stimulation of the olivocochlear region did not suppress a response in the somatic cortex to single shock of a cutaneous nerve. The neuromuscular blocking agent was found to have no effect upon the suppression.

The question arises as to whether or not some structure other than the olivocochlear bundle is also being stimulated. If the central suppression is due to the olivocochlear bundle, the possibilities are that it may have other central connections, that there may be an antidromic effect, or that there may be certain key fibers in the eighth nerve essential for a cortical-evoked potential which are being selectively inhibited (*4*).

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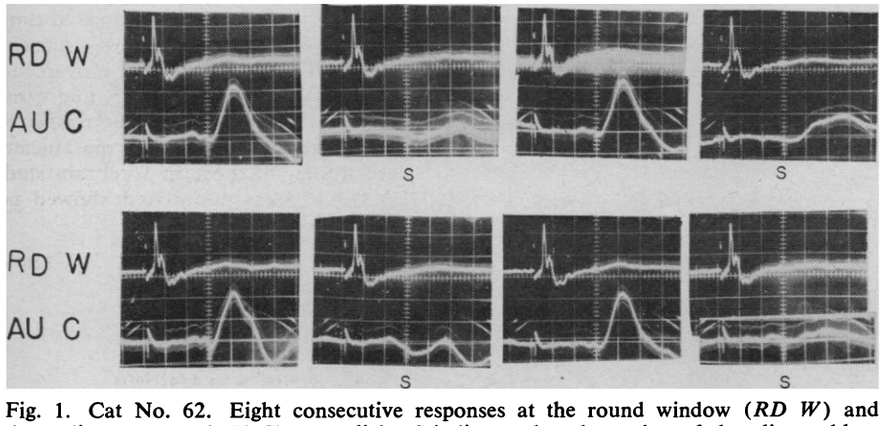

Fig. 1. Cat No. 62. Eight consecutive responses at the round window (*RD W*) and the auditory cortex (*AU C*) to a click. *S* indicates that the region of the olivocochlear bundle was stimulated with a series of shocks at 4 volts in the manner described in the text, before the click was presented. Note the suppression of the cortical response without any change in the round window response. One large division vertically is 5 μv and horizontally is 5 msec.

References and Notes

1. G. L. Rasmussen, *J. Comp. Neurol.* **84**, 141 (1946).
2. R. Galambos, *J. Neurophysiol.* **19**, 424 (1956).
3. J. E. Desmedt and K. Mechelse, *Proc. Soc. Exptl. Biol. Med.* **90**, 772 (1959).
4. This work has been supported by grants from the Alfred P. Sloan Foundation and the National Institute of Neurological Diseases and Blindness.
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