Differentiation of hypothalamic feeding and killing*

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Bipolar electrodes were chronically implanted in the posterior lateral hypothalamic-medial forebrain bundle area of male Long-Evans rats. Animals which displayed either stimulus-bound feeding or stimulus-bound killing were trained to self-stimulate and tested while given the opportunity to eat or kill during self-stimulation. Average duration of barpressing was greater in the presence of the goal object appropriate to the stimulus-bound behavior, suggesting a differentiation of hypothalamic mechanisms of feeding and killing.

It is the consensus of most investigators that the killing behavior of rats towards mice (Karli, 1956) and frogs (De Sisto & Huston, 1970; Bandler & Moyer, 1970; Johnson, De Sisto, & Koenig, 1972) are forms of predation and part of a behavior complex related to obtaining food (Barnett, 1963; Moyer, 1968).

However, there is increasing behavioral and physiological evidence that the killing behavior of the rat is reinforcing in its own right. For example, Myer and White (1965) demonstrated that rats would learn a T-maze discrimination for the opportunity to kill, and Van Hemel (1972) has demonstrated discrimination and reversal learning in an operant situation in which the reinforcement was the opportunity to kill a mouse. A number of investigators have elicited and facilitated mouse-killing and frog-killing by electrical (King & Hoebel, 1968; Karli, 1970; De Sisto & Huston, 1970; Panksepp, 1971) and chemical (Bandler, 1970; Smith et al, 1970) stimulation of various hypothalamic sites.

The above studies do not deal with the question of whether the killing mechanism is an independent neural substrate or merely a subsystem within a feeding and food-getting system. There is substantial evidence to support both views.

Karli (1956) found that natural nonkiller rats would starve to death rather than kill and eat an available mouse. Furthermore, rats will kill up to 30 frogs in a row without the opportunity to eat the prey (De Sisto & Huston, 1970; Van Hemel & Myer, 1970). Whalen and Fehr (1964) reported that cyclic food deprivation induced nonkiller rats to kill mice, and Paul et al (1971) found that the probability of killing was greater in rats that had experienced a 2-week period of cyclic food deprivation. De Sisto and Huston (1971) found that food deprivation facilitated frog-killing in natural killer rats and also delayed habituation of killing.

Hutchinson and Renfrew (1966) elicited both feeding and predatory attack from the same electrode in the lateral hypothalamus of cats. Current thresholds for

elicited killing were 200 microA above those for elicited feeding. However, the authors concluded that feeding and killing represent different topographic forms of a single hypothalamic mechanism controlling appetitive behavior.

In studies using rats, King and Hoebel (1968) found a differentiation of feeding and killing sites in the lateral hypothalamus. However, Karli (1970) and Panksepp (1971) have elicited both feeding and killing from the same electrode in the posterior hypothalamus. However, in both these experiments, animals were allowed to eat part of the mice they had killed, so that these animals had the opportunity to associate killing with feeding.

It is well known that there is close anatomical overlap of lateral hypothalamic regions where electrical stimulation elicits consummatory behaviors and regions that support self-stimulation (Glickman & Schiff, 1967). Furthermore, the opportunity to engage in a previously electrically elicited behavior has a facilitatory effect on self-stimulation through the same electrode (Coons & Cruce, 1968; Mogenson & Morgan, 1967; Mendelson, 1967).

The purpose of the present experiment was to test the effects of the opportunity to feed and kill on the average duration of barpressing during intracranial self-stimulation. If feeding and killing have separate mechanisms, one would expect that only the goal object appropriate to the previously elicited behavior would have a facilitatory effect on self-stimulation and that inappropriate goal objects would not.

METHOD

Subjects

Male hooded rats of the Long-Evans strain, weighing 150-300 g, were used. They were housed in individual cages and fed Purina Lab Chow and water ad lib.

The frogs used were *Rana pipiens*. They were 2½-3 in. in length. They were kept in a large sink containing tap water. Frogs were not fed, and under these conditions showed no loss of activity.

Electrode Implantation

Ss were anesthetized with Nembutal (40 mg/kg). Bipolar electrodes, .008 in. in diam, were aimed at the posterior lateral

*This research was supported by NIMH Grant 1 R03 MH22055-01 and a Faculty Research Grant from Colby College to the first author. Special thanks are extended to Valerie Craig and Frank Stephenson for their assistance.

Table 1
Results of Stimulus-Bound Behavior Tests and Average Barpress Duration for Each Goal Object

Rat	Behavior	S-Bound Behavior Threshold (microA)	Self- Stimulation Threshold (microA)	Average Barpress Duration (Sec)		
				No Goal	Food	Frog
10	K	12	14	2.13	1.97	3.74
10B	K FC	15	30	1.89	2.25	2.32
2A	K	7	25	1.13	1.15	2.29
5	K	14	29	1.89	1.65	3.13
6B	F FC K	30	36	2.45	2.89	2.60
162	F	11	21	1.19	2.55	1.47
183	F	10	24	1.69	2.92	1.50
8B	K FC	20	10	2.30	2.34	2.37
2B	None			1.41	1.31	1.25
4B	F, K	30	34			
3B	K	3	22			
17	K	29	34			
2	K FC	18	30			
21	F	20	—	1.65	2.05	1.52
29	F	13	—	1.89	2.54	1.43

Note—K = killing, F = feeding, FC = food carrying.

hypothalamus. The stereotaxic coordinates from the bregma were 3.5 mm posterior, 1.5 mm lateral, and 8.5-8.7 mm inferior, perpendicular to the skull. Electrodes were secured to the skull with anchoring screws and cranioplastic cement.

Stimulus-Bound Behavior Tests

Ss were first tested for stimulus-bound (S-bound) behaviors (feeding, drinking, gnawing, or frog killing). The test chamber was a 9 x 16 x 12 in. Plexiglas container with a white-noise speaker at one end. The box was covered with a transparent Plexiglas top through which the animal could be observed. A mercury swivel commutator was situated above the box. Ss were placed in the box 10 min prior to testing. The stimulation consisted of trains of 60-Hz intracranial stimulation, 20 sec on and 10 sec off. A 10-kilohm resistor was placed in series with the electrode to allow monitoring of the current through the rat brain by an oscilloscope. Purina Lab Chow pellets were spread liberally on the floor of the chamber along with a live frog and a 4 x 1½ in. block of wood. Protruding from one end of the box was the water bottle from the rat's home cage. To test for S-bound consummatory behavior, the current level was started at a low intensity and increased by 2-microA steps read base to peak of the sine wave (.707 rms). The criterion for an S-bound behavior was the initiation of the behavior within 10 sec of the onset of the stimulation and termination of it within 10 sec of the onset of the stimulation. The current level was increased until either an S-bound behavior occurred or the S showed escape behavior. Each rat was tested once a day, on 4 consecutive days. On a particular day, after an S-bound behavior was elicited, animals were given 10 additional trials at the same current level. Following these tests, a wire mesh container in which food or a live frog could be placed was mounted above the bar. This container not only allowed visual and olfactory exposure to the goal objects, but also allowed Ss to eat or kill. The programming equipment was adjusted so that the rat received continuous stimulation for as long as the bar was depressed. The number of responses and the total time the stimulation was on (i.e., the total time the bar was depressed during the session) were recorded so that an average duration could be calculated. Each rat spent three sessions a day in the test chamber—one session for each goal object. The sessions were 10 min long, and each S had at least a 20-min rest between sessions. The testing took place on 4 consecutive days, with the order in which the goal objects were presented varied from day to day. The current levels used for each rat were chosen slightly

above the threshold current for elicited behavior. By using this level, it was certain that the rat would not only respond at the bar, but at the same time would be eliciting the S-bound behavior. All the Ss had food and water ad lib in the home cage and all were given killing experience on the first day of testing with a frog placed in the home cage.

RESULTS

Table 1 shows the results of the S-bound behavior tests. Out of 30 rats which were implanted, 7 showed S-bound killing and 7 showed S-bound feeding. The range of threshold currents eliciting killing was 3-29 microA, and the range for feeding was 7-30 microA. Several of the rats showed some mixed responses: 10B and 8B showed a strong killing response and a weak feeding response at the same current level, 6B showed a strong feeding response with weaker food-carrying and killing responses, 4B showed both feeding and killing responses, 17 showed strong killing and weak food-carrying responses. A weaker response means that the response occurred less frequently than did the strong response over a 10-trial testing session.

Eleven rats were used in the self-stimulation tests: 5 were S-bound killers, 5 were S-bound feeders, and 1 showed no S-bound behavior. Rat 6B pulled his electrode cap off during the testing period and therefore only partial results were obtained. Table 1 summarizes the average duration of barpressing in all conditions for each rat. The trends that developed are quite clear and are shown graphically in Fig. 1. The S-bound killers always held the bar down longer when a frog was present than if either food or no goal object was available. The mean durations were 2.65, 1.87, and 1.87 sec, respectively. An analysis of variance showed these differences to be statistically significant ($p < .05$). The S-bound feeders all held the bar down longer when food was present than if a frog or no goal object was present.

The mean durations were 2.77, 1.86, and 1.78 sec, respectively. These differences were also statistically significant ($p < .05$). It is quite obvious that the opportunity to kill significantly affected the S-bound killers, but food had no effect whatsoever. For the S-bound feeders, the opportunity to kill had no effect (see Fig. 1). It was mentioned before that 3 Ss showed somewhat of a duality of S-bound behaviors, with one behavior stronger than the other. In these cases, the weaker behaviors had some effect on the stimulation. The two killers, 10B and 8B, who also showed weak feeding, gave mean barpress durations of 2.35, 2.29, and 2.09 sec for frog, food, and no goal object, respectively. The S-bound feeder who showed some killing response had means of 2.89, 2.60, and 2.45 sec for food, frog, and no goal object, respectively. As can be seen, the mixed response gave rise to an intermediate effect caused by the weaker response. It is significant, however, that in all cases the goal object corresponding to the stronger S-bound behavior always elicited a longer duration of barpress. A further observation was that in order for the above effects to occur, the animal actually had to engage in the S-bound behavior while pressing the bar. The mere presence of the goal object was not sufficient for elicitation of the effect.

DISCUSSION

The S-bound behavior tests yielded some interesting results. In several cases, pure responses were elicited, i.e., only killing or feeding; in other cases, there were combinations of responses elicited, usually with one response occurring with greater frequency. Many investigators (Valenstein, 1968; Von Holst & Von St. Paul, 1963; Roberts, 1969) have elicited more than one response from the same electrode at the same current level. As Roberts (1969) and Berquist (1972) have pointed out, mixed and incomplete responses to stimulation may be the result of the activation of two or more interdigitated neural mechanisms. More specific chemical stimulation (Grossman, 1962; Bandler, 1970; Smith et al, 1970) as well as electrical stimulation through smaller surface area electrodes (Olds et al, 1971) result in clear differentiation of responses.

This experiment, like others (Roberts & Kiess, 1964; Mendelson, 1967; Mogenson & Kaplinsky, 1970), has demonstrated that the stimulation not only increases the likelihood of a specific behavior, but also increases the reward value of certain related goal objects. Thus, the present experiment has clearly differentiated hypothalamic feeding and killing mechanisms, and reinforces the lesion and stimulation experiments of Karli (1971) in the rat and of Bandler (1971) in the cat, involving lateral hypothalamic and midbrain pathways, which have also clearly differentiated the feeding and killing mechanisms.

The intermediate effects obtained when a duality of

Fig. 1. Average duration of barpress for S-bound feeders and killers.

behaviors was observed would seem to indicate that the electrode was stimulating two adjacent or partially overlapping mechanisms: the unequal effects explained by unequal stimulation of the two adjacent pathways.

Mouse-killing and frog-killing are self-strengthening, response latencies decreasing over time as killing becomes more efficient (Karli, 1956; De Sisto & Huston, 1970). Killing can also be facilitated or inhibited by certain kinds of developmental experience. In the case of mouse killing, early interaction between mice and rats decreases the incidence of killing (Denenberg et al, 1964; Myer, 1969), whereas with frog killing, the opposite effect is obtained (Johnson, De Sisto, & Koenig, 1972). Facilitation of killing can be obtained by partial food deprivation (Paul et al, 1971; Whalen & Fehr, 1964) as well as the opportunity to observe killing (Johnson, De Sisto, & Koenig, 1972).

We have shown that food deprivation in combination with the opportunity to kill and eat can change electrically elicited feeding to killing. Up until the time of deprivation, Ss were never allowed to eat frogs. Other experiments involving stimulation of these same areas have obtained strong feeding and killing responses from the same electrode (Karli, 1970; Panksepp, 1971). In both these experiments, Ss had eaten mice they had killed. The suggestion is that a differentiation can be obtained only in an animal which has not had the opportunity to learn that the frog is a source of food. Of course, in a wild animal, it is likely that all laboratory conditions (food deprivation, observation) that facilitate killing are in effect.

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(Received for publication October 18, 1973;
revision received December 11, 1973.)