1972

The Effect of Consummatory Stimuli on Brain Stimulation Reinforcement: Further Differentiation of Killing and Feeding Mechanisms in the Posterior Hypothalamus of Rats

Matthew S. Zweig
Colby College

Follow this and additional works at: http://digitalcommons.colby.edu/seniorscholars
Colby College theses are protected by copyright. They may be viewed or downloaded from this site for the purposes of research and scholarship. Reproduction or distribution for commercial purposes is prohibited without written permission of the author.

Recommended Citation
http://digitalcommons.colby.edu/seniorscholars/377

This Senior Scholars Paper (Open Access) is brought to you for free and open access by the Student Research at Digital Commons @ Colby. It has been accepted for inclusion in Senior Scholar Papers by an authorized administrator of Digital Commons @ Colby. For more information, please contact enrhodes@colby.edu.
The Effect of Consummatory Stimuli on Brain Stimulation Reinforcement:

Further Differentiation of Killing and Feeding Mechanisms in the Posterior Hypothalamus of Rats

by

Matthew S. Zweig

Submitted in partial fulfillment of the requirements for the Senior Scholars Program
Colby College
1972
Approved By:

Michael J. Bredis
Tutor

James M. Gillespie
Major Department Chairman

E. Pauling Johnson
Reader

George A. Haier
Senior Scholars Committee, Chairman
Abstract

Traditionally, killing or aggressive behavior has been viewed as an operant performed to gain reinforcement such as food. There is, however, increasing evidence indicating that killing is reinforcing in itself. Myer and White (1965) and Van Hemel (1970) have shown that natural killing behavior can be used to reinforce the learning of a discrimination. Roberts and Kiess (1964) implanted electrodes in the anterior hypothalamus of natural non-killing rats and elicited killing behavior. They showed that this electrically elicited killing could also be used to reinforce the learning of a discrimination. Thompson (1963,1964) demonstrated that both Siamese fighting fish and fighting game cocks would perform an operant to see a conspecific and give their species-typical aggressive display. Tellegren et al. (1969) showed that fighting mice will choose the arm of a T-maze which contained a mouse which they could attack.

The relationship between feeding and killing has been thought to be a very close one. However, there has been a controversy in the literature as to whether killing is controlled by feeding and therefore a sub-system of a feeding mechanism or whether it is an independent system in itself. Karli (1956) showed that natural killers would not eat the prey they had killed and natural non-killers would starve to death rather than kill. Von Hemel and Meyer (1970) and DeSisto and Huston (1970) found that natural killing rats would kill up to 30 mice and frogs without ever having the opportunity to eat them. Whalen and Fehr (1964) and Paul et al. (1971) have shown that cyclic food deprivation could increase the frequency of killing in a group of rats. Heimstra (1965) was not
able to induce killing with cyclic food deprivation. Roberts and Kiess (1964) showed that hungry cats, from whom they were electrically elicited killing, would immediately leave a bowl of food to kill a rat when electrical stimulation was turned on. Hutchinson and Renfrew (1966) were able to elicit both feeding and killing from the same electrode although elicitation of killing was always at a higher current level. King and Hoebel (1968), DeSisto and Huston (1971) never observed feeding in stimulus-bound killers during stimulation and never observed killing in stimulus-bound feeders. Karl and Vergnes (1964) showed that when both feeding and killing were abolished by rostral to caudal bilateral lesions within the hypothalamus, killing recovered before feeding in all cases. Thus killing took place with no feeding.

The focus of the present set of experiments was to further clarify the relationship between killing and feeding mechanisms in the hypothalamus. Male Long-Evans hooded rats were implanted with bipolar electrodes aimed at the posterior lateral hypothalamus. They were tested for S-bound behaviors and S-bound feeders and killers were used in the experiments. The subjects were then trained to bar press. They received stimulation for as long as the bar was held down. Then either food, live frog, or no goal object was placed above the bar and the rat was allowed to bar press and engage in an S-bound behavior simultaneously. The average bar press duration was recorded for each rat. The rats were run both food satiated and food deprived. A preference test was then run. Two bars were mounted at the end of the box and either no goal object, food, or frog were placed above each bar in various combinations. The
rat was placed in the box and allowed to press at either bar.

The results were quite clear. The live frog and thus an opportunity to kill elicited longer durations of bar press for the S-bound killers than did the food or no goal object. For the S-bound feeders, the food elicited the longer duration. The results were unaffected by food deprivation. Thus, the effects of feeding and willing were differentiated in this experiment. The one S-bound killer run in the preference test showed a clear preference for the bar that had the frog over it.

These findings suggest that killing is in fact a mechanism in itself and one that is distinct from the feeding mechanism.
Introduction

The technique of electrical stimulation of the brain with chronically implanted electrodes was first developed by W.R. Hess in 1928. Using this technique, James Olds and Peter Milner (1954) found that when the electrode was placed in various parts of the diencephalon of an animal, the animal would perform an operant, that is, pressing a bar, in order to receive the stimulation. In fact, it was found that the animals would respond at the rate of up to 4,000 responses an hour and would continue to respond up to the point of exhaustion. From these observations, it was concluded that the stimulation had reinforcing properties, that is, it could be used to increase the probability of an operant behavior when applied to certain areas of the brain.

Further studies on the effects of brain stimulation have demonstrated that the stimulation could cause the animal to engage in various consummatory behaviors or fixed action patterns (for example, feeding, drinking, growing, and aggressive behavior); because these responses came under control of the electrical stimulation, they were called stimulus-bound behaviors (see Glickman & Schiff, 1967 for review). Von Holst and Von Saint Paul (1962), using chickens as subjects, were able to elicit any behavior pattern which the chicken had been observed to perform naturally. These included preening, stretching of the neck, scratching with one foot, eating, drinking, and escape behavior.

After discovering that the stimulation could elicit various behaviors, the next step was to discover exactly what was being stimulated, i.e., was the electrode stimulating a specific pathway for each elicited be-
havior or rather a non-specific neural substrate mediating all the behaviors. Von Holst and Von Saint Paul, in the study previously cited, were able to elicit several different behavior patterns from the same electrode. Hutchinson and Renfrew (1966) elicited feeding and attack from the same electrode, although attack was elicited at a higher current level. Feeding and drinking points were found in the posterior lateral hypothalamic region overlapping those areas which elicited male copulatory behavior (Caggiula, 1970; Caggiula & Hoebel, 1966). Grossman (1962) showed that there is some specificity between hunger and thirst by demonstrating that either could be blocked as well as elicited by injecting either cholinergic or adrenergic agents through the same cannulae in the hypothalamus. Valenstein, Cox, and Kakolewski (1970) have advanced a non-specificity hypothesis. They base their conclusions on their experimental results which showed that initial S-bound behaviors could be easily modified. Animals were first screened for S-bound feeding, drinking, or gnawing. After this had been ascertained, the initial goal object was replaced by another. The authors found that in virtually every case, with sufficient stimulation sessions with the new goal object, the new S-bound behavior would emerge. Furthermore, when the initial goal object was later placed in the test chamber along with the new one, both S-bound behaviors were elicited with approximately the same frequency. They concluded that hypothalamic stimulation seemed to excite a substrate for a group of responses rather than for any single response.

Roberts (1969) has adopted a view of specificity of hypothalamic mechanisms and has tried to offer an explanation for some of the phenomena
cited above. He feels that mixed responses elicited from the same electrode may be the result of the non-specificity of the electrical stimulation. This is quite likely in view of the fact that independent brain mechanisms often overlap or are closely adjacent, especially in such a densely packed structure as the hypothalamus. The current spread from the electrode tip may therefore by stimulating two or more independent mechanisms at the same time, resulting in the observed mixed response. By using a more specific type of stimulation, Roberts felt that differentiation could be accomplished. Sixty Hz stimulation of the preoptic and anterior hypothalamus of the oppossum elicited grooming, mating behavior, attack, eating, exploration, and escape-like activity. Localized radio frequency diathermic warming acts selectively on thermo-receptor neurons in this area. When this more specific stimulation is applied only grooming is elicited. Thus, differentiation can be shown to be present when more specific types of stimulation are used. Roberts then went on to experimentally test Valenstein's results of the modifiability of hypothalamically-elicited responses. The initial S-bound screening was done by placing various goal objects in the test chamber one at a time (Valenstein had placed them all in at the same time.) This procedure resulted in many rats showing two or three initial responses; Valenstein almost always got only one response. Rats having electrodes which elicited one or two oral responses (eating, drinking, or gnawing) were given seven nights of training with one of the ignored goal objects. The hypothesis was that if an appreciable number of missing responses could not be trained, or if trained were significantly weaker than the initial preferred response, then Valen-
stein's non-specific substrate theory would have to be ruled out. The results of the experiment were that out of 12 rats, 6 showed no evidence of new responses, although they continued to perform the initial response. The other 6 rats developed weak responses that in no case reached the performance level of the initial response. Thus, if the initial screening test is a single object test so that as many responses as possible can be detected, then the remaining ignored responses cannot be trained or can only be weakly trained. Roberts concludes that this evidence is incompatible with Valenstein's single non-specific substrate, but consistent with the hypothesis of overlapping but specific mechanisms.

The above experiments clearly demonstrate that the question of specificity versus non-specificity is still a wide open one and that much more work needs to be done to conclusively answer it.

It has been mentioned that attack or killing behavior has been elicited from areas of the hypothalamus. Further explanation of this phenomenon is necessary at this point. Animals, such as cats and rats, can be classified into two categories; natural killers and natural non-killers. Using rats as an example, a natural killer is one who will kill a mouse when the mouse is placed in the rat's home cage. A natural non-killer will not kill the mouse, ten to twenty percent of laboratory rats are natural killers (Karli, 1956), 42 percent kill chicks, 90 percent kill turtles (Bandler and Moyer, 1970), and 100 percent kill frogs (DeSisto and Huston, 1970; Bandler and Moyer, 1970). It might be asked how one can elicit frog killing in rats if they all kill frogs naturally. This can be answered by a clarification of terminology. One elicits killing
from those animals who are natural non-killers and "facilitates" killing from those who are natural killers. Here "facilitate" means that the killing comes under the control of the stimulation and the animal will kill faster and more often during the stimulation. It should be pointed out that since all animals feed and drink naturally, these behaviors are facilitated by stimulation and not elicited.

Traditionally, killing has been taken as an operant performed in order to receive reinforcement such as food or escape from a painful situation (Skinner, 1966). Killing, in this case is merely a means to an end. Another view of killing is that it is not an act which is reinforced; rather, it is reinforcing in itself. There is increasing evidence which supports this view. Myer and White (1965) showed that rats who were natural killers would learn a discrimination with the opportunity to kill used as the reinforcement. The rats were screened for killing by placing a mouse in the rat's cage on three successive days and two mice successively on the following three days. Rats were also screened in a similar manner for killing rat pups, and were never allowed to eat a killed animal. Rats were divided into two groups; 10 which killed mice but not rat pups and 10 which killed neither. The set-up was a T-maze with a mouse in one arm and a rat pup in the other. Rats were given killing experience and maze training in the maze set-up prior to the testing. With the arm containing the mouse designated as the correct choice, the natural killers eventually chose correctly 80-85 percent of the time. Their running speed also increased on successive tests. It was concluded that the killing was indeed reinforcing, that is, it could be used in the teaching of
just as food has been used in teaching a hungry animal to learn a maze, press a bar, or make a discrimination.

A study by Roberts and Kiess (1964) showed that the killing behavior elicited by electrical stimulation was also reinforcing. Before surgery, cats were screened for natural killing of rats. Only the natural non-killers were chosen for surgery. Multiple electrodes were implanted in the anterior hypothalamus of these cats. After recovery from surgery, the cats were tested for elicited stimulus-bound killing, i.e., killing a rat during the stimulation. Only those cats which showed relatively pure and sustained attacks were chosen for the experiment. The set-up in this study was a Y-maze with a rat in one arm. With the stimulation on, all the cats learned to go to the correct, i.e., the side containing the rat. When the rat was placed in the opposite arm, 3 of the cats were able to learn this reversal; the others were unable to learn it. With the stimulation off there were no attacks and the cats ignored the rats. The authors concluded

"the learning evidenced in the maze indicates that when a readiness for predatory attack is aroused in cats by hypothalamic stimulation, the overt performance of the attack becomes positively reinforcing."

Killing used as reinforcer for learning an operant response, a key press, was shown by Von Hemel (1970). Natural mouse-killing rats were used in the experiment. The test chamber contained two keys and a mouse dispenser. During the screening period, mice were given to the rats on various schedules. Four rats which quickly and consistently killed mice were chosen for further study. The rats were shaped to key press by the presentation of a mouse after they had pressed either key. After shaping,
there were seven days of discrimination tests during which a mouse was presented only after the subject pressed the "correct" key. This was followed by seven days of reversal testing. Results were as follows: for both the discrimination and the reversal each rat made fewer errors on the final six days than they did on the first. These findings confirm those of Myer and White. However, in this case the rats not only learned the initial discrimination, but also the reversal.

Thompson (1963,1964) demonstrated that both Siamese fighting fish and fighting game cocks would perform operants for the opportunity to see a conspecific and give their species-typical aggressive display, and Tellegen et. al. (1969) showed that fighting mice will choose the arm of a T-maze which contained a mouse which they could attack.

The preceding studies suggest that killing is a reinforcing act in itself and can be used to increase the frequency of learning some operant task. What these studies do not deal with, however, is the question of whether the killing mechanism is an independent neural substrate or merely a sub-system within a feeding and food getting system. This relationship has presented much difficulty in the past several years. There exists substantial data to support both views. For example, Karli (1956) found that natural killers would not eat the prey they had just killed and natural non-killers would starve to death rather than kill and eat a mouse. Von Hemel and Meyer (1970) found that natural killing rats would kill at least 30 mice in succession without ever having the opportunity to eat them. DeSisto and Huston (1970) found that rats would kill up to 30 frogs in a row without the opportunity to eat them. Whalen and Fehr (1964) col-
lected data which seemed to link feeding and killing. They found that cyclic food deprivation could significantly increase the frequency at killing in a group of rats. Heimstra (1965), however, found that he was unable to induce killing in non-killer rats by the use of cyclic food deprivation. Paul, Miley, and Baenninger (1971) found results which supported the Whalen and Fehr findings. Two strains of rats were used; male Long-Evans bred for killing and Sprague-Dawley rats randomly bred. The subjects in the first series of tests were the Long-Evans rats. The experiment was in four phases with tests for mouse killing conducted after each. Phase A: All subjects were given free access to food for six days. Phase B: Half of the subjects were placed on a 23 hour food deprivation schedule for 15 days while the other half had food ad lib for that period. Phase C: Half the subjects given free food in phase B were placed on 23 hour deprivation schedule and the other half was given 15 more days with food ad lib, half of the food deprived rats in phase B were given food ad lib for the next 15 days while the other half was maintained on the deprivation schedule. Phase D: All subjects were given free food for 28 days. The group that was food deprived in both phase B and phase C showed an increase in killing frequency from an initial 55 percent to 100 percent. The group which was deprived in phase B showed an increase from 30 percent to 100 percent after the deprivation period. The group which was deprived in phase C showed an increase of 18 percent to 82 percent. The group which was satiated throughout the testing period showed some incidental increase, but it was not nearly as significant as the others. In the second experiment, Sprague-Dawley rats were used. One group was continuously satiated while the other group was starved for two days and then
maintained on a 23 hour food deprivation schedule for 13 days. All animals had food ad lib for the following 15 days. For this strain of rats the initial killing frequency was much lower than was exhibited in the Long-Evans strain. In this case there was some increase in the frequency of killing, but it was nowhere as large as the increase found with the Long-Evans rats. Nevertheless, the data of these two experiments seem to indicate that there is some connection between feeding and killing behavior.

Another experiment in the Robert and Kiess paper (1964) dealt with the effects of hunger on the killing behavior elicited by electrical stimulation. After two days of training to eat in the test box, the subjects, cats, were food deprived for 48 hours and placed in the test chamber with a bowl of food and a rat. While the subjects were eating the stimulation was turned on for 15 seconds. The latency to terminate eating, to initiate attack, and the duration of attack and eating were recorded. Subjects stopped eating with a median latency of .3 seconds, attacked in 6.3 seconds, and maintained the attack for a mean duration of 4.7 seconds. None of the subjects returned to eating while the stimulation was on. The conclusion drawn here was that there seemed to be a clear differentiation between the feeding and killing mechanism. Hutchinson and Renfrew (1966) obtained data which implied a somewhat different conclusion. The subjects were adult male cats who showed no killing or attack behavior when presented with a rat in preliminary tests. Two to six monopolar electrodes were placed in the lateral hypothalamus of each cat. Subjects were food satiated at all times. First the cats were presented with rats and the threshold for the elicitation of attack behavior was taken by increasing the current
intensity stepwise from 10-50 ua. Following this a threshold was taken for feeding behavior. If any spontaneous feeding occurred in the test chamber the test was halted until a twenty minute period of no eating had passed. It was found that from each electrode which had elicited attack, feeding was also elicited, however, in every case the threshold for feeding was lower than that for killing. The authors concluded that the area of the hypothalamus where stimulation elicits attack is principally responsible for the mediation of appetative behavior and, furthermore, the attack behavior elicited from this area represents a particular form of food acquisition. The authors did not feel that the killing was elicited because of current spread from a feeding pathway to a killing pathway brought on by the necessity of using a higher current. Rather, they felt that the lateral hypothalamus, which is responsible for food acquisition and ingestion, may direct signals, most probably via fibers of passage, to some further removed areas where the attack behavior is mediated. Contrary results were obtained by King and Hoebel (1968). All subjects were natural non-killers, screened by placing a mouse in the home cage for a period of 1 to 24 hours on each of at least seven days. Electrodes were implanted in the anterior lateral hypothalamus. Each rat was placed in a chamber which contained a drinking tube, blocks of wood, Purina food pellets, and 1-5 mice. Stimulation was begun at a low current level and increased in small steps until the rat ate, drank, gnawed, killed a mouse, or the current level became so high that the rat attempted to escape. Seven rats killed mice during the stimulation. None of these animals were ever ob-
served to eat, drink, or gnaw during stimulation. Rats that were S-bound feeders never showed any type of attack behavior when presented with a mouse instead of food. This led the authors to conclude that there was a definite neural substrate controlling killing in the hypothalamus of the rat.

Some very convincing evidence for the existence of an independent killing mechanism comes from Karli and Vergnes (1964). They abolished the killing response in rats by making large rostral to caudal bilateral lesions within the lateral hypothalamus. These lesions not only abolished the killing response, but also the feeding behavior. The fact that lesions of the lateral hypothalamus produce aphagia, i.e., no eating behavior, was previously established by Teitelbaum and Epstein (1962). Karli and Vergnes found that if the animal later recovered oriented behavioral activities, the recovery of the killing response always preceded that of the feeding by days and sometimes weeks. Thus, killing behavior was able to take place even though the animal remained in a state of complete aphagia.

What the above survey of the literature clearly demonstrates is that there is great confusion concerning the relationship of killing and feeding. There has been much data collected, but the conclusions drawn are contradictory. Obviously, further work must be done in this area and this is the focus of the present series of experiments.

Rationale of Present Experiments

Electrical stimulation of some sites in the brain gives rise to both rewarding and punishing effects (Olds, 1962; Bower and Miller, 1958;
Valenstein, 1963). That is, the subject will perform an operant to turn the stimulation on and then a few seconds later will make another response to turn it off. Many of these sites lie in the lateral hypothalamus, an area where the stimulation also elicits a variety of consummatory behaviors (feeding, drinking, growing). Mendelson (1969) used these two facts and studied the effects of various goal objects on the onset of the aversive qualities of the stimulation. Subjects were rats with electrodes implanted in the lateral hypothalamus. Two criteria had to be met by rat in order to be used in the experiment. First, the stimulation had to elicit eating, drinking, or gnawing at a current intensity between 5-60 ua. Second, the stimulation had to induce escape behavior within 15 seconds at a current intensity between the threshold for the elicited behavior and 60 ua. The test box was a shuttle box with microswitches at both ends under the floor of the chamber. These controlled the onset and the offset of the stimulation. The animals weight on either side of the box controlled the switches. The animals were tested with and without the appropriate goal object in the box. Time spent on the "on" side of the box was recorded. In the empty shuttle box the median "on" duration was 4-20 seconds. With the introduction of the goal objects, the "on" duration was increased by at least 50 percent and the range was 12-233 seconds. The combined median duration in the empty box was 14 seconds and with goal objects it was 33.5 seconds. It is clear that the presence of the proper goal object delays the onset of the aversive effects of the stimulation.

Coons and Cruce (1968) studied the effects of food on the threshold for self-stimulation. Subjects were rats with electrodes implanted in the
lateral hypothalamus. The rats were tested for S-bound behaviors and those that showed S-bound feeding were used in the experiment. First, the threshold current, i.e., the lowest current that will support self-stimulation was measured with food available right next to the bar. Second, the food was removed and the threshold measured again. It was found that with the food present, the rats would self-stimulate for a lower current level than if food was not present.

Mogenson and Kaplinsky (1970) studied the effects of goal objects on reinforcing electrical stimulation. Subjects were rats with electrodes implanted in the lateral hypothalamus. The animals were screened for S-bound behaviors. The test chamber had two bars mounted at the end of the box 6 inches apart. Stimulation was administered for as long as the rat held the bar down. The appropriate goal object for each rat was placed next to one of the bars. The rat was placed in the box and allowed to press either bar. The results were that in all cases the rats preferred the bar with the goal object and furthermore, the duration of each bar press was longer for the bar which had the goal object next to it.

The present set of experiments is based on the data obtained in the above studies and by using the techniques employed in them, it is hoped that more light is shed upon the relationship between feeding and killing.

Method

Subjects

Male hooded rats of the Long-Evans strain weighing 150-300 grams 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 inches 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**

Subjects were anesthetized with sodium nembutal (40 mg/kg). Bipolar electrodes, .008 inches in diameter, were aimed at the posterior lateral hypothalamus. The stereotaxic coordinates from the bregma were 3.5 mm posterior, 1.5 mm lateral, and 8.5-8.7 inferior, perpendicular to the skull. Electrodes were secured to the skull with anchoring screws and cranioplastic cement.

**Stimulus-bound Behavior Tests**

Subjects 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" plexiglass container with a white noise speaker at one end. The box was covered with a transparent plexiglass top through which the animal could be observed. A mercury swivel commutator was situated above the box. Subjects were placed in the box 10 minutes prior to testing. The stimulation consisted of trains of 60Hz intra-cranial stimulation 20 seconds on and 10 seconds off. A 10k ohm 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" 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 1 ua 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 seconds of the onset of the stimulation and termination of it within 10 second of the offset of the stimulation. The current level was increased until either an S-bound behavior occurred or the subject showed escape behavior. Each rat was tested once a day on four consecutive days.

Results

Table 1 shows the results of the S-bound behavior tests. Out of twenty five rats which were implanted, 7 showed S-bound killing and 5 showed S-bound feeding. The range of threshold currents eliciting killing was 3-29 ua and the range for feeding was 7-30 ua. 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.

Self-Stimulation Training and Threshold Tests

Subjects were shaped to bar press for electrical stimulation by method of successive approximations. The current level was sufficiently high enough to maintain a steady rate of response by the subject. For each bar press, the rat received .5 seconds of 60 Hz sine wave current. The rats were allowed to make several hundred responses at the bar to complete the training.

A current threshold for maintainence of the bar press response was then measured. The criterion chosen for the threshold current was that
Table 1. RESULTS OF STIMULUS-BOUND BEHAVIOR TESTS, AND AVERAGE BAR PRESS DURATION FOR EACH GOAL OBJECT

<table>
<thead>
<tr>
<th>Rat</th>
<th>Behavior</th>
<th>S-bound threshold</th>
<th>self stimulation threshold</th>
<th>average bar press no goal</th>
<th>duration frog</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>K</td>
<td>12ua</td>
<td>14ua</td>
<td>2.13</td>
<td>1.97</td>
</tr>
<tr>
<td>10B</td>
<td>K FC</td>
<td>15ua</td>
<td>30ua</td>
<td>1.89</td>
<td>2.25</td>
</tr>
<tr>
<td>2A</td>
<td>K</td>
<td>14ua</td>
<td>29ua</td>
<td>1.13</td>
<td>1.15</td>
</tr>
<tr>
<td>5</td>
<td>K</td>
<td>14ua</td>
<td>29ua</td>
<td>1.89</td>
<td>1.65</td>
</tr>
<tr>
<td>6B</td>
<td>F FC K</td>
<td>30ua</td>
<td>36ua</td>
<td>2.45</td>
<td>2.89</td>
</tr>
<tr>
<td>162</td>
<td>F</td>
<td>11ua</td>
<td>21ua</td>
<td>1.19</td>
<td>2.55</td>
</tr>
<tr>
<td>183</td>
<td>F</td>
<td>10ua</td>
<td>24ua</td>
<td>1.69</td>
<td>2.92</td>
</tr>
<tr>
<td>8B</td>
<td>K FC</td>
<td>20ua</td>
<td>10ua</td>
<td>2.30</td>
<td>2.34</td>
</tr>
<tr>
<td>2B</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4B</td>
<td>F,K</td>
<td>30ua</td>
<td>34ua</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3B</td>
<td>K</td>
<td>3ua</td>
<td>22ua</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>K</td>
<td>29ua</td>
<td>34ua</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>K FC</td>
<td>18ua</td>
<td>30ua</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

K=killing  F=feeding  FC=food carrying
current for which the subject would make 10 or less responses within a 5 minute period. The initial current was high enough to support a steady rate of responding and then was reduced by 2 ua steps after every 10th response until the threshold criterion was met. The threshold test was taken once a day on four consecutive days.

Results

The range of threshold currents was 14-36 ua. In all cases except rat BB, the current threshold for self-stimulation was higher than that for the elicitation of the S-bound behavior.

Experiment I

The purpose of this experiment was to test the effects of food and the opportunity to kill on electrical stimulation in S-bound feeders and killers. The hypothesis was that for the S-bound killers the opportunity to kill would delay the onset of the aversive effects of the stimulation while food has no effect. The opposite would occur for the S-bound feeders.

Procedure

A cage was mounted above the bar in which food, a live frog, or no goal object was placed. 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 3 sessions a day in the test chamber; one session for each goal object. The sessions were ten minutes long and each subject had at least a 20 minute rest between sessions. The testing took place on four
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 self-stimulation as previously determined. This level was chosen because the threshold for self-stimulation has been shown to be greater than the threshold for elicitation of the S-bound behavior. This was shown in the threshold tests which we took and it was also shown by Huston (1971) and Mendelson (1971). Thus, by using this level, it was certain that the rat would respond at the bar and at the same time would be eliciting the S-bound behavior. All the subjects had food and water ad lib in the home cage and all were given killing experience on the first day of testing by placing a frog in the home cage.

Results

Nine rats were used: 5 were S-bound killers, 3 were S-bound feeders, and one showed no S-bound behavior. Rat #68 pulled his electrode cap off during the testing period and therefore only partial results were obtained. Table I summarizes the average duration of bar-pressing in all conditions for each rat. The trends which developed are quite clear and are shown graphically in Figure 1. 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 seconds, 1.87 seconds, and 1.87 seconds respectively. An analysis of variance (Table 2), showed these differences statistically significant (pc.05). The S-bound feeders all held the bar down longer when food was present than if a frog or no goal object were present. The mean durations were 2.77 seconds, 1.86 seconds, and 1.78
<table>
<thead>
<tr>
<th>Duration (secs.)</th>
<th>S-bound Killers</th>
<th>S-bound Feeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig 1. AVERAGE DURATION OF BAR PRESS FOR S-BOUND FEEDERS AND KILLERS

bar press duration secs.

no food frog goal object

---------

= S-bound killers

- - - - - - - - = S-bound feeders
### Table 2

<table>
<thead>
<tr>
<th>Source</th>
<th>Df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subjects</td>
<td>9</td>
<td>22.3</td>
<td>.2</td>
<td>.075</td>
</tr>
<tr>
<td>Types</td>
<td>1</td>
<td>0.2</td>
<td>.2</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>8</td>
<td>22.1</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td>Situation</td>
<td>2</td>
<td>6.8</td>
<td>3.4</td>
<td>4.363*</td>
</tr>
<tr>
<td>Situation-Types</td>
<td>2</td>
<td>6.5</td>
<td>3.2</td>
<td>4.161*</td>
</tr>
<tr>
<td>Error</td>
<td>16</td>
<td>12.5</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Sessions</td>
<td>3</td>
<td>1.7</td>
<td>0.6</td>
<td>1.705</td>
</tr>
<tr>
<td>Sessions-Types</td>
<td>3</td>
<td>1.9</td>
<td>0.6</td>
<td>1.960</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>7.8</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>Situations-Sessions</td>
<td>6</td>
<td>3.7</td>
<td>0.6</td>
<td>2.804*</td>
</tr>
<tr>
<td>Situations-Sessions-Types</td>
<td>6</td>
<td>2.6</td>
<td>0.4</td>
<td>1.905</td>
</tr>
<tr>
<td>Error</td>
<td>48</td>
<td>10.5</td>
<td>0.2</td>
<td></td>
</tr>
</tbody>
</table>

Types = S-bound feeders and killers  
Situations = no goal object, food, frog  
Sessions = 1, 2, 3, 4  
* = Significant at .05 level
seconds respectively. These differences were also statistically signifi­
cant (pc.05). It is quite obvious that the opportunity to kill signi­
cantly effected the S-bound killers, but food had no effect whatsoever. For the S-bound feeders, the opportunity to kill had no effect (See Figure 1). It was mentioned before that 3 subjects 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 stimu­
lation. The two killers, 108 and 88, who also showed weak feeding, has mean bar press durations of 2.35, 2.29, and 2.09 seconds 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 seconds for food, frog, and no goal object, respectively. As can be seen, the mixed res­
ponse 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 bar press. A further observation was that in order for the above effects to occur, the animal actually had to engage in the S-bound be­
havior while pressing the bar. The mere presence of the goal object was not sufficient for elicitation of the effect. A more systematic investi­
gation of this finding is needed however.

Experiment II

The purpose of this experiment was to see if subjects showed only preference for the bar which had the appropriate goal object above it.

Procedure

Two bars were mounted six inches apart at the end of the test chamber.
Each bar had a cage mounted above it as housing for the goal objects. Before the testing, each subject had sufficient training at each bar to control any initial preference. Each subject was then tested in the following situations: 1) no goal object over one bar, live frog over the other 2) no goal object over one bar, food over the other 3) food over one bar, live frog over the other. Tests were conducted on four consecutive days with the positions of the goal objects varied and sequence of situations varied. Each session lasted 10 minutes with at least 20 minutes between sessions. All subjects had food and water ad lib in the home cage at all times.

Results

Only one rat could be successfully trained to consistently switch back and forth between the two bars; that is, show no initial preferences for either bar. This animal was run through only one set of sessions. The subject was an S-bound killer. There was a clear preference shown for the bar which had the frog over it rather than the bar with either the food or no goal object. In the no goal object-frog situation, there were 16 responses at the no goal object bar and 75 responses at the frog bar. In the food-frog situation there were 48 responses at the food bar and 112 responses at the frog bar. In the food-no goal object situation there were 217 responses at the no goal object bar and 150 responses at the food bar.

Experiment III

The purpose of this experiment was to see whether food deprivation would have any effect on the data obtained in Experiment II; more spe-
cifically, whether the food deprivation would cause the killers to hold the bar down longer for the food rather than the frog.

**Procedure**

The procedure was the same as in experiment II except that the subjects were food deprived for 24 hours prior to testing. Two days of testing were held with several days in between to allow the rats to recover from the initial deprivation period.

**Results**

Three S-bound killers were tested. The mean durations for no goal object, food, and frog were 2.15, 1.59, 2.10 seconds, respectively. There was a significant change here in that the no goal object situation elicited the longest mean duration; however, the frog situation still elicited a longer duration than did the food and furthermore, the rats never fed on the food when it was available in the testing situation.

**Histology**

After completion of the experiments, subjects were sacrificed with an overdose of sodium nembutol and perfused intracardially with isotonic saline and 10 percent formalin. Brains were frozen and 35 micron sections were cut and stained with cresyl violet.
Discussion

The S-bound behavior tests yielded some interesting results. In several cases pure responses were elicited, i.e., only killing or feeding. However, in many other cases there were combinations of responses elicited, usually with one response occurring with greater frequency. Some of the combinations observed were mentioned in the results section. From the points we were stimulating, there was never any S-bound drinking. Mixed responses have been observed before by Hutchinson and Renfrew (1966), although in that case they were elicited at different current levels. Valenstein (1970), Von Holst and Von Saint Paul (1962) and Roberts (1969) have all observed several responses elicited from the same electrode at the same current level. Clearly, these observations, while interesting in themselves, do not give us any more of a clue as to what hypothalamic system or systems are actually being stimulated when the behaviors are elicited.

Experiment I demonstrated that an S-bound killer will administer electrical stimulation to himself for longer durations when there is an opportunity to kill than if there is no goal object present. The experiment further showed that the presence of food had no effect on the stimulation, i.e., it had about the same average duration as the no goal situation. In light of the results obtained by Mendelson (1969) and the fact that the opportunity to kill elicited a longer duration of stimulation, it seems that first, the act of killing has rewarding effects and second, killing is controlled by a neural mechanism in much the same way that feeding and killing are controlled. The implications of the experiment
are more far reaching than those just stated. The major implications pertain to the specificity-non-specificity controversy. The experiment has clearly differentiated the effects of the opportunity to kill and the opportunity to eat. Taking this one step further, it has differentiated the feeding and killing mechanisms. If one was to adopt Valenstein's theory of a non-specific substrate, it would seem that the differentiation shown in the present study would be impossible simply because of the lack of differentiation in Valenstein's hypothesized substrate. Certainly, if the electrode was simply making this substrate more sensitive to external goal objects than the feedback from both the food and the opportunity to kill should have the same rewarding effects. Experiment I shows this not to be the case. This is a striking result considering the close relationship which has normally been assumed to exist between feeding and killing. The intermediate effects obtained when a duality of behaviors was observed in initial S-bound behavior tests would seem to indicate that the electrode was stimulating two adjacent or partially overlapping mechanisms. The unequal effects are explained by an unequal stimulating of the two pathways, i.e., the electrode may have been close to one rather than the other causing unequal distribution of the stimulation.

Based on the results of this experiment, it seems that the idea of separate but overlapping or adjacent pathways, at least for feeding and killing, offers the best view of what is happening physiologically.

In light of the fact that Mogenson and Kaplinsky (1970) were able to train many rats to press at two adjacent bars and get switching from bar to bar, it seems unusual that we were only able to train one rat successfully in Experiment II. However, this rat, who was a strong S-bound
killer, showed a clear preference for the bar with the frog over it rather than the bar with food or no goal object. If any conclusions can be drawn at all from data on a single rat, it would have to be that the opportunity to kill the frog was more rewarding than either the stimulation alone or the food and stimulation. It is clear that the preference here must be studied further.

The food deprivation experiment, Experiment III, yielded some significant results. Although there was an unexplained increase in the durations elicited by the no goal situation, the S-bound killers still held down the bar longer when a frog was available than if food was available. Furthermore, none of the rats tested ever fed on the food during the testing situation. This is consistent with the Roberts and Kiess (1964) findings. That hungry cats who were S-bound killers immediately left a bowl of food to kill a rat when stimulated. The difference in our experiment was that the rats didn't feed during the stimulation even though a frog was not present for them to kill. It is interesting to note that one rat, #2B, who was tested only on the first day and who displayed no S-bound behaviors, began to feed towards the end of the testing session. Of the S-bound killers, only #10 fed on the frog it had just killed, the other 2 did not.

In conclusion, these three experiments do not support Valenstein's non-specific substrate hypothesis. Experiment I showed that there is a differentiation in the rewarding effects of food and the opportunity to kill. Experiment II implied that for S-bound killers there is a clear-cut preference for stimulation and a frog rather than stimulation and food. Experiment III showed that even though S-bound killers were highly
motivated for food because of 24 hours of deprivation, the differentiated effects of food and the opportunity to kill obtained in Experiment I were still present. The theory of overlapping and adjacent pathways controlling feeding and killing could account for the results obtained in these experiments, while the non-specific substrate theory runs into many obstacles in accounting for the data.


Karli, P. and Vergnes, M. Dissociation experimentale du comportement


