AMYGDALOID STIMULATION AND OPERANT REINFORCEMENT IN THE RAT

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Electrical stimulation of chemically implanted electrodes in 62 rats tested for self-stimulation and escape behavior indicated a topographical division of the amygdala along classical anatomical lines. Most electrodes yielding self-stimulation alone and most electrodes yielding highest self-stimulation rates were in the central and medial nuclei of the corticomedial division. Most electrodes yielding escape alone and all those yielding the highest escape rates were proximal to the lateral and basal nuclei of the basolateral division. Effects were not strictly localized; distribution of approach and escape overlapped, with peaks in the corticomedial and basolateral divisions, respectively. All stimuli yielded mild self-stimulation and escape effects, frequently from the same electrode. Self-stimulation rates were moderate but escape rates high compared with brain stem.

Operant reinforcement may be positive or negative, depending on whether the basic direction of behavior is toward or away from the reinforcing stimulus. Electrical stimulation applied directly to the brain in tegmentum, diencephalon, and telencephalon often has one or the other or both of these effects. The results of stimulation depend usually on the anatomical locus to which the stimulus is applied, but sometimes on the parameters of stimulation or on other characteristics of the electrical stimulus or the behavioral test (Olds, 1962).

It is generally agreed that the amygdaloid complex is a correlating or modulating structure within the brain's system of motivational and emotional mechanisms (Gloor, 1960). But the relation of amygdaloid stimulation to the distinction between positive and negative reinforcement is unclear. A number of studies have indicated that amygdaloid stimulation elicits aversive responses progressing from mild to intense depending on the intensity or duration of stimulation (Urin & Kaada, 1960). The group of studies taken together produce a strong impression that negative reinforcement might be expected on stimulation of most points in the amygdaloid complex. The words used to describe the behaviors involved include "fear," "anxiety," and "defensive reactions." At milder levels of stimulation, alerting, and attention were observed culminating in escape and flight on the one hand and anger and fury on the other as the stimulus intensity increased.

In view of this series of observations suggesting negative reinforcement, made mostly on the rat, it was somewhat surprising that a preliminary mapping of positive reinforcement effects, even though done on the rat and monkey (Brady, 1961; Brunst & Delgado, 1968; Olds, 1956; Wurts & Olds, 1966) found amygdala and amygdaloid complex among the primary regions yielding approach reactions—i.e., positive reinforcement of behavior. The yield of positive reinforcement might have been anticipated on the basis of earlier work reporting observation of sniffing reactions, no reaction or attention unaccompanied by fear or anger (Urin & Kaada, 1960), eating and food-related activities, and female sexual reactions (Benedict, 1960). Instead these studies emphasized the aversive and aggressive effects observed, and positive reinforcement was not anticipated.

Areas previously thought to yield mainly
aversive effects (e.g., Maser, 1942) have recently been discovered to yield rewarding effects upon electrical stimulation (Olds & Olds, 1965; Roberts, 1958). This discovery makes it clear that although elicited responses which suggest aversion can easily be found, it is much more difficult to find elicited responses which suggest that the animal is being positively reinforced by a particular stimulus or state. It is here that operant measures have been most useful in transforming presynaptic data into a system of empirical and metric observations; for they allow definition and quantification of both positive and negative reinforcement in terms of the same continuous variable—namely, the rate of freely emitted operant behavior.

The present study was aimed at an anatomical analysis of the amygdaloid complex of the rat into functionally meaningful subsystems. The anatomical position of electrodes was used as the primary independent variable and positively and negatively reinforcing effects as dependent variables. The aim was to find whether a reasonable anatomical differentiation of the amygdala into positive and negative reinforcing systems would appear.

Method

Electrode Placement

One bipolar electrode was implanted in each of 79 male albino rats. The electrode was formed by twisting together two silver wires, each 0.25 mm. in diameter and pretrained with Formvar insula-
tion except for the cross-cut section of the tips. In most cases the tips were separated only by their insulation (a distance of from 56-1 mm.), although a few tips were spaced slightly farther apart. Both electrode wires were connected to a metal terminal on a plastic block screwed to the skull.

Electrodes were directed at predetermined points in the amygdaloid complex: anterior-posterior, lateral, and vertical coordinates were determined from the atlases of de Groot (1899) and König (1936). General surgical procedures for electro-
ode implantations were routine and have been summarized by Olds and Milner (1954). A small burr hole was drilled in the skull at the designated anterior-posterior and lateral coordinates with bregma and the midline midsagittal plane as reference points. The electrode wires were cut to a length such that when they were lowered through the burr hole, their tips would correspond to designated ver-
tical coordinates. The 5s were allowed at least 1 week for recovery.

Behavioral Procedures

Approach test. The self-stimulation test described by Olds and Milner (1954) was used. The S was placed in a 5 x 11 in. rectangular box, which was 10 in. high and had a 4 X 4 in. pedestal extending out of the short wall. For each pedal depression, S received through the implanted electrode a 60-cycle sine wave stimulus train of 1-msec, maximum duration.Whatever the pedal was released in less than 2 sec, the stimulus was terminated without the release.

A preliminary period of training lasting about 2 weeks preceded the testing sessions. For purposes of training, Ss were placed in the box and the stimulus current level was set at 50 µA, . The Ss received the stimulus when they depressed the bar in the course of their exploratory activities. (The range of "random" bar pressing rates—those recorded when no stimulus reward was given—was 10-46 responses per hour.) The minimum bar pressing rate taken as indicative of reward was 50 responses per hour, that is, 80 responses per 8-

min. period. On each day during training, Ss were run for an average of 8 min. periods at 50 µA. Like the training sessions, the testing sessions consisted of six 8-min. stimulation periods. Stimula-
tion intensity was increased successively for each period: 5, 10, 20, 30, 40, and 50 µA. This permitted a determination of self-stimulation threshold, i.e., of the current level at which S began to press the bar. Testing was continued for at least 2 weeks, or until a stable curve of responding was achieved.

The self-stimulation scores reported in the fol-

lowing sections are based on data obtained in the last week of testing. For each S, the range of self-
stimulation for the last 3 days of testing was plotted as a function of electrical current. Later, to get a single index of behavior for each S, the upper limit of this plotted range was used. The logic of this procedure is as follows: although many factors might have been lowering the rates of bar pressing (for example, distractions in the room or increasing fatigue from the stimulating current), no obvious factors were oper-
ating to raise the rates. Moreover, because the same procedure was used for all Ss, the upper limit of the response frequency range provides a satisfactory basis for comparison.

Escape test. A modified Sidman test was used (Olds & Travis, 1960). In this test S depressed a bar to terminate the stimulus. A programmer de-

livered a 60-cycle sine wave stimulus train once per second, and by a pedal response S could terminate or postpone the series for 4 sec. Then the stimulus was delivered again, and con-

tinued until S depressed the bar for another 4 sec. break. Although the original test as described by Sidman was an avoidance rather than an escape test, the behavior elicited in the present study was attrib-
uted to an escape from the stimulus because the 3-sec. interval between the stimulus and the
Behavioral Procedures

Approach test. The self-stimulation test described by Olds and Milner (1954) was used. The S was placed in a 5 x 11 in rectangular box, which was 90 in high and had a 4 in. pedestal extending out of the short wall. For each period depression S received through the implanted electrode a 60-cycle sine wave stimulus train of 3-msec. maximum duration. Whenever the pedal was depressed in the first 3 sec., the stimulus was terminated with the release. A preliminary period of training lasting about 2 weeks preceded the testing sessions. For purposes of training, Ss were placed in the box and the stimulus current level was set at 50 µa. max. The Ss received this stimulus when they depressed the pedal in the center of their exploratory activity. The range of “random” bar pressing rates—those recorded when no stimulus reward was given—was 50-90 responses per hour. The minimum bar pressing rate taken as indicative of reward was 600 responses per hour, that is, 40 responses per 5-min. period. On each day during training, Ss were run for six consecutive 5-min. periods at 50 µa.

Like the training sessions, the testing sessions consisted of six 5-min. stimulation periods. Stimulus intensity was increased monotonically for each period: 5, 10, 20, 30, 40, and 50 µa. This permitted a determination of self-stimulation threshold, i.e., of the current level at which S began to press the bar. Testing was continued for at least 2 weeks, or until a stable curve of responding was achieved.

The self-stimulation scores reported in the following sections are based on data obtained in the last week of testing. For each S, the range of self-stimulation was determined by the approach test in which testing was plotted as a function of electric current. Later, to get a separation between the Ss, the upper limit of this plotted range was used. The logic of this procedure was as follows: although many factors might have been lowering the rate of bar pressing (for example, distractions in the room or increased muscle mass in the brain from the stimulating current), no obvious factors were operating to raise the rates. Moreover, because the same procedure was used for all Ss, the upper limit of the response frequency range provided a satisfactory basis for comparison.

Escape test. A modified Sidman test was used (Olds, 1956a). Testing began at 8 a.m. and continued until 5 p.m. for a total of 4 days. The escape test was designed to terminate the stimulus. A programmer delivered a 50-cycle, maximum-current 3-msec. train once per second, and by a pedal response S could terminate or postpone the session for 4 sec. Then the stimulus was delivered continuously until S depressed the bar for another 3-msec. break. Although the original test as described by Sidman was an avoidance rather than an escape test, the behavior elicited in the present study can be attributed to an escape from the stimulus because the 3-msec. interval between the stimuli and the 4-sec. interval between a response and a shock (when a response occurred) were so short (see Sidman, 1955). The total number of seconds S escaped the stimulus was recorded; a minimum of 160 sec. escaped during an 8-min. period was taken to indicate effective effort of stimulation.

For the escape as for the approach test, training preceded testing, and continued for at least 2 weeks. The training procedure once again consisted of six 5-min. intervals each day. During the initial training period, the current was set successively at levels of 5, 10, 15, 20, 25, and 30 µa.

The Ss that yielded no escape responses under this regimen were shifted to higher current levels: 5, 10, 20, 30, 40, and 50 µa.

In testing, the appropriate stimulus schedule was used for high- and low-threshold Ss; thus it was possible to avoid subjecting Ss to repeated stimulation at excessive current levels. The range of escape scores for the last week of testing was plotted as a function of electric current, the upper limit again being taken as a simple index of each S's behavior.

Electrode Insertion

After testing had been completed, Ss were perfused with physiological saline followed by 15% formol saline. The brains were removed and further fixed in formalin for at least 30 hr. Frozen sections of the brain 40 µm thick were stained with cresyl violet to determine the anatomic location of the electrode tips.

Results

As was observed in studies on rat diencephalon (Olds & Olds, 1963), it was observed in the present study of the amygdala that behavior resulting from stimulation at one point fell into one of four categories: (a) Approach but no escape (i.e., in the approach test S reached the criterion of 50 bar presses in an 8-min. period but in the escape test failed to meet the criterion of 180 sec. escaped in an 8-min. period); (b) escape but no approach; (c) both approach and escape from the same electrode; and (d) neither approach nor escape. The categories are labeled “play,” “minus,” “plus-minus,” and “neutral,” respectively. Data illustrating them are presented in Figure 1.

At the top of this figure are photomicrographs of four histological sections, each of which shows a sample electrode placement yielding one kind of result. The ranges of approach and escape responses obtained when each sample electrode was stimulated at the various electric current levels are plotted below the relevant histological sections.

Frequency of the Four Stimulation Effects

Of the 79 electrodes successfully implanted in the temporal lobe area, 42 were in the amygdala. A total of 37 electrodes were tested for both approach and escape, 6 having been lost before escape tests were made. Self-stimulation with no marked escape was observed in 13 cases; escape with no marked self-stimulation was observed in 6 cases; and approach and escape behavior both above the respective criteria were observed in 17 cases. Only 2 of the electrodes subjected to both tests yielded neither self-stimulation nor escape. Thus 95% of the amygdaloid electrodes yielded motivational effects—either approach or escape or both.

Table 1 summarizes the approach data, with response rates categorized as high, moderate, and low. To facilitate comparison of these approach data with those yielded by brain-stem electrodes, the categories are roughly the same as those used in an earlier paper on the diencephalon (Olds & Olds, 1963). No amygdaloid electrode yielded approach behavior at a high response rate.

Table 2 summarizes the escape data from the present experiments, with response rates again categorized as high, moderate, and low.

Topographical Organization

Differences between stimulation effects yielded by electrodes in different nuclear areas do appear. Nearly all 13 electrodes yielding approach behavior but no escape behavior fell in close proximity to the central and medial nuclei, as illustrated in Figure 2. Of these 12 cases, 4 were clearly in the medial nucleus, 5 were on the boundaries of the central nucleus, 1 lay between the central and the medial nuclei, and 3 were in the ventromedial area. (The ventromedial area encompasses the cortical nuclei, the medial basal nucleus, and probably the lateral aspect of the medial nuclei, all of which appear nearly homogenous in the histological sections.) Only one electrode yielding minus effects fell in the central and medial nuclei,
and it was close to the escape-yielding putamen. Moreover, relatively few of the electrodes which fell in the central and medial nuclei yielded plus-minus effects. Thus, the area yielding the strongest self-stimulation and yielding nearly all cases of unequivocal approach behavior seems to be coterminous with the central and medial nuclei in the corticomedial division. All other nuclear areas in the amygdala also yielded self-stimulation but seldom with the intensity of points in the central and medial nuclei and usually in conjunction with escape at the same electrode. Thus most of them fall into the plus-minus category. The three plus points which fell outside the central and medial nuclei lay in the ventromedial area, and this area is usually characterized by plus-minus effects. Except for one case yielding moderate approach, stimulation via electrodes in the lateral basal and lateral nuclei yielded low approach behavior or none at all, and in all three cases stimulation yielded escape behavior as well. Electrodes in the lateral basal and lateral nuclei yielded the most marked escape behavior. Of the five electrodes yielding minus behavior (see Figure 2), two were dorsally placed near the boundary of the caudate-
putamen; one of these was dorsal in the lateral nucleus of the amygdala and the other just dorsal to the central nucleus of the amygdala. The other three electrodes yielding this behavior appeared to be related to the basolateral area of the amygdala; one was just below the lateral basal nucleus, another between the lateral basal and lateral nuclei, and the third in the lateral nucleus. Furthermore, of the plus-minus electrodes, all three yielding high escape rates were in or close to the basolateral area, as were three of the five yielding moderate escape rates. Therefore the basolateral division can be said to yield most of the minus behavior in the amygdala and a generally higher rate of escape responding as well.

Plus-minus electrodes yielding low escape rates were found mainly in the ventromedial area, as were the other two plus-minus electrodes yielding moderate escape rates.

The difference between approach and escape rates in medial, ventromedial, and lateral placements is illustrated in Figure 3. Each of the 37 electrode placements tested for both approach and escape was classified according to the rate categories (high, moderate, low, or none) into which the approach and escape scores fell. Of the electrodes in the central and medial group 80% yielded greater approach than escape and only 7% yielded greater escape than approach. These relationships were reversed in the lateral nuclear group.

### Table 1
**Frequency of Approach Behavior in 22 Amygdaloid Placements Which Meet the Approach Criterion**

<table>
<thead>
<tr>
<th>Rate of self-administration in 8-hr period</th>
<th>No. of electrodes yielding only approach behavior (15-min period)</th>
<th>No. of electrodes yielding escape-inhibition behavior</th>
<th>No. of electrodes yielding both approach and escape behavior</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (Above 300)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Moderate (260-300)</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Low (Below 200)</td>
<td>11</td>
<td>13</td>
<td>1</td>
<td>25</td>
</tr>
</tbody>
</table>

78% yielded greater escape and no electrode yielded greater approach than escape.

Other Placements

Although electrodes were directed toward the amygdaloid proper, some placements were found to be scattered in surrounding structures.

Anterior amygdaloid and adjoining areas.

In this anterior section both approach and escape behavior were yielded by the 13 electrodes; they were too sparsely distributed to form any clear pattern, however. The only electrode in the entire study which yielded high approach behavior was located near the medial forebrain bundle. The two electrodes in the anterior amygdaloid area which yielded plus behavior were ventrally placed, and one electrode was proximal to the nucleus of the lateral olfactory tract.

Hypocampus. One of the electrodes in this area yielded plus and minus behavior; one yielded minus behavior, one yielded plus behavior, and two yielded neutral behavior.

**Claustrum or piriform cortex.** Two electrodes in this area yielded plus minus behavior with low approach and moderate escape; one yielded low plus behavior, and one yielded moderate minus behavior.

**Caudate-putamen.** Eight of the nine elec-
Fig. 2. Anatomical location of 79 electrodes in the amygdala and surrounding structures. (There are four types of squares to indicate the self-stimulation rate obtained from a point, and four types of circles indicate the escape rate obtained from the same point. An unpaired square or circle indicates that only one test was performed. Sections are modified from de Groot, 1959, and are arranged in an anterior-to-posterior order. Abbreviations: AAA, anterior amygdaloid area; ABL, amygdaloid lateral basal nucleus; ACE, amygdaloid central nucleus; AL, amygdaloid lateral nucleus; AME, amygdaloid medial nucleus; AVM, amygdaloid ventromedial area; CE, external capsule; CI, internal capsule; CLA, claustrum; CPU, caudate/putamen; GP, globus pallidus; HPC, hippocampus; IGL, intercalated nucleus; MFB, medial forebrain bundle; MOE, nucleus of the olfactory tract; OT, optic tract; PIR, piriform cortex; SO, supramarginal nucleus; ST, striatum terminalis; V, lateral ventricle.)
trodes in this area yielded escape behavior. Of those eight, five yielded moderate or high escape rates. Four of the eight escape electrodes also yielded approach behavior. The ninth point in the area was neutral.

**Thresholds**

Approach behavior usually occurred at thresholds of 20 or 30 μA, although there were a few cases in which it occurred at thresholds of 10 or 40 μA. The range and distribution of thresholds for escape behavior were similar. No topographical pattern is obvious in the threshold data.

**Seizures**

Of the 42 Ss with amygdaloid placements, seizures were observed frequently in more than half the cases. The data did not suggest a topographical localization of seizures in any one part of the amygdala, but there was a slight tendency for implantations in the medial and central nuclei, which yielded higher rates of approach behavior, to be free of seizures.

**Discussion**

The Role of the Amygdala in Brain-Stem Reinforcement Mechanisms

Evidence from previous studies suggests that a pair of mechanisms—one related to negative reinforcement and the other to positive reinforcement—exists in a tegmental-to-thalamic system on the one hand and a lateral hypothalamic system on the other (Olds & Olds, 1963). Electrical stimulation in the tegmental-thalamic system yields negative reinforcement; electrical stimulation in the lateral hypothalamic system yields positive reinforcement; and electrical stimulation in the medial nuclei of the hypothalamus yields both negative and positive reinforcement at the same point.

Inspection of the present data shows that negative reinforcement alone was quite frequent with electrodes in areas of the basolateral ganglia and hippocampus, which are proximal to the amygdala. Points yielding strong negative reinforcement were found along the boundary of the basolateral division. Positive reinforcement alone appeared frequently with electrodes on the medial edge of the amygdala and surrounding structures. (These data were obtained from a point, and four types of same point. An unpaired square or circle indicates that they were obtained from dura mater; other data were obtained from amygdaloid area; ARL, amygdaloid lateral; AL, amygdaloid lateral nucleus; AME, amygdaloid area; C, external capsule; CI, internal capsule; caudate nucleus; hippocampus; ICL, intercalated cells of the olfactory tract; OT, optic tract; PIB, terminalis; V, lateral ventricle.)
terior (amygdaloid) and to the posterior (tegmento-diencephalic) subdivisions.

To make a reasonable guess, one should carefully weigh the different outcomes of comparable experiments involving amygdala and hypothalamus. Positive reinforcement experiments have indicated differences in rate of responding (Olds, 1956) and satiation (Olds, 1958) between behavior directed toward hypothalamus and behavior directed toward amygdaloid stimulation. In the hypothalamic cases, rates are abnormally high and there is far less tendency to normal satiation; moreover, the positive reinforcement is accompanied by excitation rather than by the pacification that normally accompanies positive reinforcement (Olds, 1962; Roberts, 1958). In amygdaloid cases, stimulation yields effects more like those of normal environmental rewards on all three counts.

Lesion experiments involving eating and sexual behavior indicate another difference. With amygdaloid lesions, there is a loss of influence on the animal by objects in the environment—at least a change of influence by objects in the environment. The animal's hunger is no longer particularly directed toward food (Kliver & Bucy, 1939); but his sexual behavior is no longer particularly directed toward sexual objects (Green, Clemente, & de Groot, 1957); and, in monkeys, there is no longer directed toward the trained places (Kliver & Bucy, 1939).

With hypothalamic lesions, there is instead loss of motivational control by the basic physiological states of the organism. This is evidenced particularly by experiments indicating a failure to eat when hungry (splanchnic), or a failure to stop eating when satiated (hyperphagia) (Attand, 1961).

Thus, the reinforcement data suggest that normal environmental rewards have effects more similar to amygdaloid stimulation than to hypothalamic stimulation. The lesion data suggest that environmental objects may exert motivational effects via the amygdaloid complex. Both types of data might lead one to guess that the amygdaloid complex contains a "projection area" for environmental rewards and punishments. If it does, the hypothalamic mechanism might be more sensitive to the internal or chemical state of the organism or might serve as something of a final common pathway in motivational control of operant behavior, a pathway not normally affected directly by environmental stimulation.

Such a view suggests that control of behavior by hypothalamic stimulation might not be dependent on amygdaloid mechanisms (a suggestion borne out by the experiments of Ward, 1961; Fernandes de Mollina & Husmanperger, 1962), but that amygdaloid control of behavior might nevertheless be dependent on some intact hypothalamic mechanisms.

Analyses of Discrepancies

There are undoubtedly a number of reasons why work on the cat suggests negative reinforcement so strongly. The physiological work of Gloer (1955) demonstrates that, from a functional viewpoint, the projections of the amygdala change if electrical stimulation of the amygdala endures over a period of time. In particular, Gloer shows that pathways open from amygdala to hippocampus and to some ventromedial hypothalamic areas while a repetitive train of 10 or more e.p.s. endures for 15 min. or more. In addition, the work of Conrady, and Brady (1959) shows that electric stimulation of an amygdaloid point in a monkey may be converted from yielding positive to yielding negative reinforcement by the production of an amygdaloid seizure. The possibility must be kept in mind, therefore, that long stimulation of some amygdaloid points—points which initially yield positive reinforcement—produces a seizure-like phenomenon and subsequently yields negative reinforcement.

An anatomical problem relates particularly to the study of Wilkinson (1962), who finds only negative reinforcement from amygdaloid stimulation. His study of cats closely resembles this study of rats; all points were tested by operant techniques, with brief stimulus trains used for both positive and negative reinforcement. Thus, arguments based on poor behavioral analyses or on special physiological effects of enduring stimuli do not apply in this case. One possibility, that Wilkinson may have missed the medial group altogether, sug-
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fects itself strongly. Since the corticoencephal and basolateral groups are about equally proportioned in the rat but the corticoencephal group is proportionally much smaller in the cat, 6 is much more likely to miss the latter group in the cat. Moreover, in the rat, where total volume is smaller and the two groups are side by side, current might easily spread to the medial group and yield positive reinforcement even if electrodes were placed in boundary regions of the lateral group. This would be far less likely to occur in the cat, where volumes are larger and the medial group is dorsally placed. Of randomly placed amygdaloid electrodes in the rat, at least half are almost certain to yield self-stimulation; whereas it is possible that a small group of similar electrodes in the cat, none would yield the effect.

REFERENCES


