of the ten runs were forced; that is, by blocking successive pairs of the three paths, the rat was forced down each of the three paths once. The remaining seven runs were free. After two days, this type of forcing was discontinued. In the remaining training period, the method was to block path 1 at the entrance one to five times daily for a total of 32 runs, leaving the rats a choice of path 2 or 3.

Test period. Five insight runs were given on the day after the last of the training runs. The swinging door at the end of path 1 was blocked, and the two gates in path 1 were let down, permitting the animal's return. The second gate of path 2, the place where it joins path 1, was not let down; this prevented the rat's return by path 2, and *S* had to return to the starting point, and then take path 2 or 3.

RESULTS AND DISCUSSION

The results of the insight runs for both groups are shown in Tables 1 and 2. These results are amazingly similar. In each group, all but one of the rats picked path 3 on the first insight run. Over 50 per cent of the rats in each group picked path 3 the second time. Two from each group picked path 3 on all five insight runs.

On the forced runs on which path 1 was blocked at the entrance, the average preference for path 2 in comparison with path 3 was 90.8 per cent for group I and 90.4 per cent for group II. Three rats chose path 2 all the time. An interesting fact is that of these three only one picked path 2 on the first insight run.

It is significant that four rats chose path 3 every time on the insight runs, especially as their average preference for path 2 on the blocked runs was over 90 per cent. A comparison between the performance on the first trial in the training series for which gate 1 was blocked at the entrance and the performance on the first insight trial showed that on the former no animal in group I chose path 3 and 18 per cent in group II chose path 3, whereas on the latter 90 per cent of group I chose path 3 and 91 per cent of group II chose path 3.

If insight is defined as one-trial learning which is subsequently maintained, then this definition is not applicable here, as the data indicate a sharp loss in performance on trial 2 and subsequent trials. This necessitates a redefinition of insight. These data also suggest that the performance might be explained in terms of other concepts such as Hull's (3) reactive inhibition.

SUMMARY AND CONCLUSIONS

The purpose of this experiment, based on Tolman and Honzik's "insight in rats" experiment, was to see if introducing an elevated cue at the intersection of paths 1 and 2 would aid the rats in grasping the fact that paths 1 and 2 had a common section leading to the goal.

The following conclusions may be drawn from this experiment:

1. On the first insight run 19 of the 21 rats chose path 3, although over 90 per cent had chosen path 2 on the forced runs.
2. Four rats chose path 3 on all five insight runs.
3. The results suggest that the introduction of a cue into Tolman and Honzik's maze may have aided the animals in grasping that paths 1 and 2 have a common section leading to the goal.
4. This experiment supports Tolman's conception of insight or inference as he used the term in his experiment, i.e., as perceptual organization that occurs when the total situation is not present.

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Received February 3, 1954.

POSITIVE REINFORCEMENT PRODUCED BY ELECTRICAL STIMULATION OF SEPTAL AREA AND OTHER REGIONS OF RAT BRAIN[1]

JAMES OLDS[2] AND PETER MILNER

McGill University

Stimuli have eliciting and reinforcing functions. In studying the former, one concentrates on the responses which come after the stimulus. In studying the latter, one looks mainly at the responses which precede it. In its reinforcing capacity, a stimulus increases, decreases, or leaves unchanged the frequency of preceding responses, and accordingly it is called a reward, a punishment, or a neutral stimulus (cf. 16).

Previous studies using chronic implantation of electrodes have tended to focus on the eliciting functions of electrical stimuli delivered to the brain (2, 3, 4, 5, 7, 10, 12, 14). The present study, on the other hand, has been concerned with the reinforcing function of the electrical stimulation.[3]

METHOD

General

Stimulation was carried out by means of chronically implanted electrodes which did not interfere with the health or free behavior of *Ss* to any appreciable extent. The *Ss* were 15 male hooded rats, weighing approximately 250 gm. at the start of the experiment. Each *S* was tested in a Skinner box which delivered alternating current to the brain so long as a lever was depressed. The current was delivered over a loose lead, suspended from the ceiling, which connected the stimulator to the rat's electrode. The *Ss* were given a total of 6 to 12 hr. of acquisition testing, and 1 to 2 hr. of extinction testing. During acquisition, the stimulator was turned on so that a response produced electrical stimulation; during extinction, the stimulator was turned off so that a response produced no electrical stimulation. Each *S* was given a percentage score denoting the proportion of his total acquisition time given to responding. This score could be compared with the animal's extinction score to determine whether the stimulation had a positive, negative, or neutral reinforcing effect. After testing, the animal was sacrificed. Its brain was frozen, sectioned, stained, and examined microscopically to determine which structure of the brain had been stimulated. This permitted correlation of acquisition scores with anatomical structures.

Electrode Implantation

Electrodes are constructed by cementing a pair of enameled silver wires of 0.010-in. diameter into a Lucite block, as shown in Figure 1. The parts of the wires which penetrate the brain are cemented together to form a needle, and this is cut to the correct length to reach the desired structure in the brain. This length is determined from Krieg's rat brain atlas (11) with slight modifications as found necessary by experience. The exposed cross section of the wire is the only part of the needle not insulated from the brain by enamel; stimulation therefore occurs only at the tip. Contact with the lead from the stimulator is made through two blobs of solder on the upper ends of the electrode wires; these blobs make contact with the jaws of an alligator clip which has been modified to insulate the two jaws from one another. A light, flexible hearing-aid lead connects the clip to the voltage source.

The operation of implantation is performed with the rat under Nembutal anesthesia (0.88 cc/Kg) and held in a Johnson-Krieg stereotaxic instrument (11). A mid-line incision is made in the scalp and the skin held out of the way by muscle retractors. A small hole is drilled in the skull with a dental burr at the point indicated by the stereotaxic instrument for the structure it is desired to stimulate. The electrode, which is clamped into the needle carrier of the instrument, is lowered until the flange of the Lucite block rests firmly on the skull. Four screw holes are then drilled in the skull through four fixing holes in the flange, and the electrode, still clamped firmly in the instrument, is fastened to the skull with jeweler's screws which exceed the diameter of the screw holes in the skull by 0.006 in. The electrode is then released from the clamp and the scalp wound closed with silk sutures. The skin is pulled tightly around the base of the Lucite block and kept well away from the contact plates. A recovery period of three days is allowed after the operation before testing. Figure 2 is an X-ray picture of an electrode in place.

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[1] The research reported here was made possible by grants from the Rockefeller Foundation and the National Institute of Mental Health of the U.S. Public Health Service. The authors particularly wish to express their thanks to Professor D. O. Hebb, who provided germinal ideas for the research and who backed it with enthusiastic encouragement as well as laboratory facilities and funds. The authors are also grateful to Miss Joann Feindel, who performed the histological reconstructions reported here.

[2] National Institute of Mental Health Postdoctorate Fellow of the U.S. Public Health Service.

[3] The present preliminary paper deals mainly with methods and behavioral results. A detailed report of the locus of positive, negative, and neutral reinforcing effects of electrical brain stimulation is being prepared by the first author.

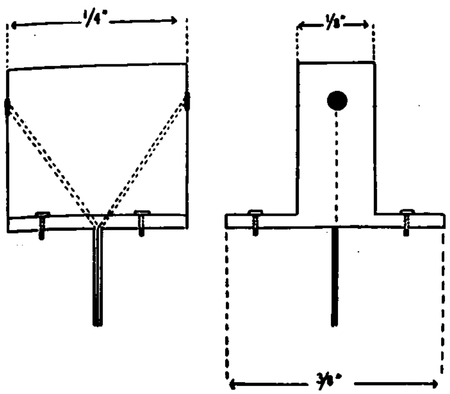

FIG. 1. Electrode design (see text for detailed description)

Testing

The testing apparatus consisted of a large-levered Skinner box 11 in. long, 5 in. wide, and 12 in. high. The top was open to allow passage for the stimulating lead. The lever actuated a microswitch in the stimulating circuit so that when it was depressed, the rat received electrical stimulation. The current was obtained from the 60-cycle power line, through a step-down transformer, and was adjustable between 0 and 10 v. r.m.s. by means of a variable potentiometer. In the experiments described here the stimulation continued as long as the lever was pressed, though for some tests a time-delay switch was incorporated which cut the current off after a predetermined interval if the rat continued to hold the lever down. Responses were recorded automatically on paper strip.

On the fourth day after the operation rats were given a pretesting session of about an hour in the boxes. Each rat was placed in the box and on the lever by *E* with the stimulus set at 0.5 v. During the hour, stimulation voltage was varied to determine the threshold of a "just noticeable" effect on the rat's behavior. If the animal did not respond regularly from the start, it was placed on the lever periodically (at about 5-min. intervals). Data collected on the first day were not used in later calculations. On subsequent days, *Ss* were placed in the box for about 3½ hr. a day; these were 3 hr. of acquisition and ½ hr. of extinction. During the former, the rats were allowed to stimulate themselves with a voltage which was just high enough to produce some noticeable response in the resting animal. As this threshold voltage fluctuated with the passage of time, *E* would make a determination of it every half hour, unless *S* was responding regularly. At the beginning of each acquisition period, and after each voltage test, the animal was placed on the lever once by *E*. During extinction periods, conditions were precisely the same except that a bar press produced no electrical stimulation. At the beginning of each extinction period, animals which were not responding regularly were placed on the lever once by *E*. At first, rats were tested in this way for four days, but as there appeared to be little difference between the results on different days, this period was reduced to three and then to two days for subsequent animals. Thus, the first rats had about 12 hr. of acquisition after pretesting whereas later rats had about 6 hr. However, in computing the scores in our table, we have used only the first 6 hr. of acquisition for all animals, so the scores are strictly comparable. In behavioral curves, we have shown the full 12 hr. of acquisition on the earlier animals so as to illustrate the stability of the behavior over time.

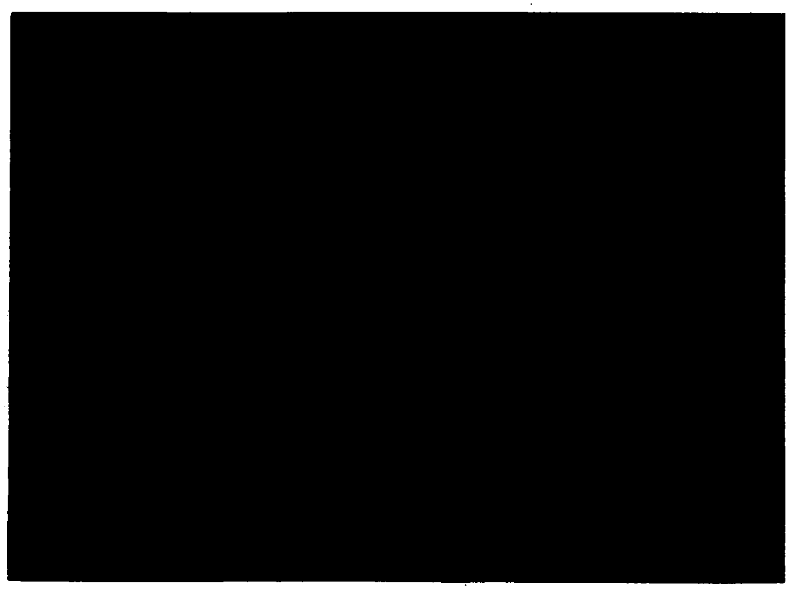

FIG. 2. X ray showing electrode in place in intact animal. There are two wires insulated completely from each other, stimulating the brain with their tips.

At no time during the experiment were the rats deprived of food or water, and no reinforcement was used except the electrical stimulus.

Animals were scored on the percentage of time which they spent bar pressing regularly during acquisition. In order to find how much time the animal would spend in the absence of reward or punishment, a similar score was computed for periods of extinction. This extinction score provided a base line. When the acquisition score is above the extinction score, we have reward; when it is below the extinction score, we have punishment.

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Determination of Locus

On completion of testing, animals were perfused with physiological saline, followed by 10 per cent formalin. The brains were removed, and after further fixation in formalin for about a week, frozen sections 40 microns thick were cut through the region of the electrode track. These were stained with cresyl violet and the position of the electrode tip determined. Figure 3 is a photomicrograph showing the appearance of the electrode track in a stained and mounted brain section.

RESULTS

Locus

In Table 1, acquisition and extinction scores are correlated with electrode placements.

FIG. 3. Photomicrograph showing the electrode track in a cresyl-violet-stained brain section. The section is 1 mm. in front of the anterior commissure. The electrode protruded through the lateral ventricle and its stimulating tip was in the septal area.

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M-4	septal	2.3–4.8	88	13
40	c.c.	.7–1.1	6	3
41	caudate	.9–1.2	4	4
31	cingulate	1.8	37	9
82	cingulate	.5–1.8	36	10
36	hip.	.8–2.8	11	14
3	m.l.	.5	0	4
A-5	m.t.	1.4	71	9
6	m.g.	.5	0	31
11	m.g.	.5	0	21
17	teg.	.7	2	1
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KEY: *c.c.*, *corpus callosum*; *hip.*, hippocampus; *m.l.*, medial lemniscus; *m.t.*, Mammillothalamic tract; *m.g.*, medial geniculate; *teg.*, tegmentum.

Figure 4 presents the acquisition scores again, this time on three cross-sectional maps of the rat brain, one at the forebrain level, one at the thalamic level, and one at the mid-brain level. The position of a score on the map indicates the electrode placement from which this acquisition score was obtained.

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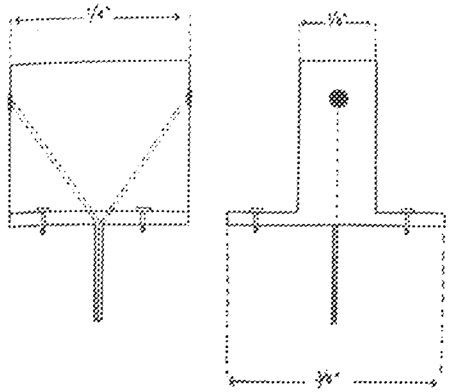

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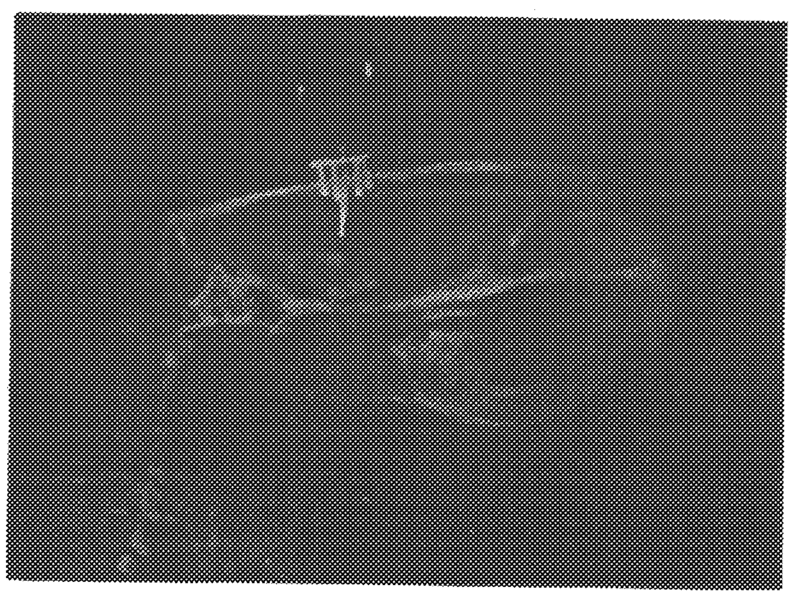

FIG. 2. *X ray* showing electrode in place in intact animal. There are two wires insulated completely from each other, stimulating the brain with their tips.

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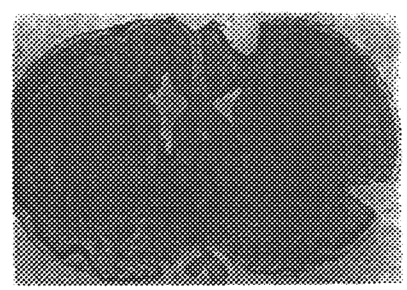

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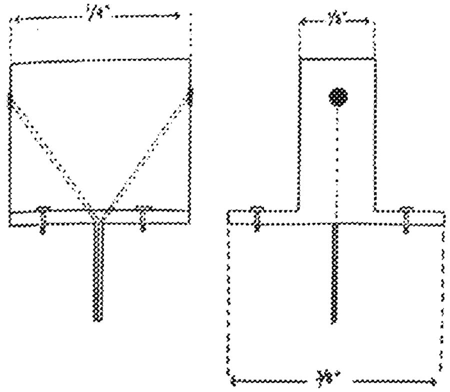

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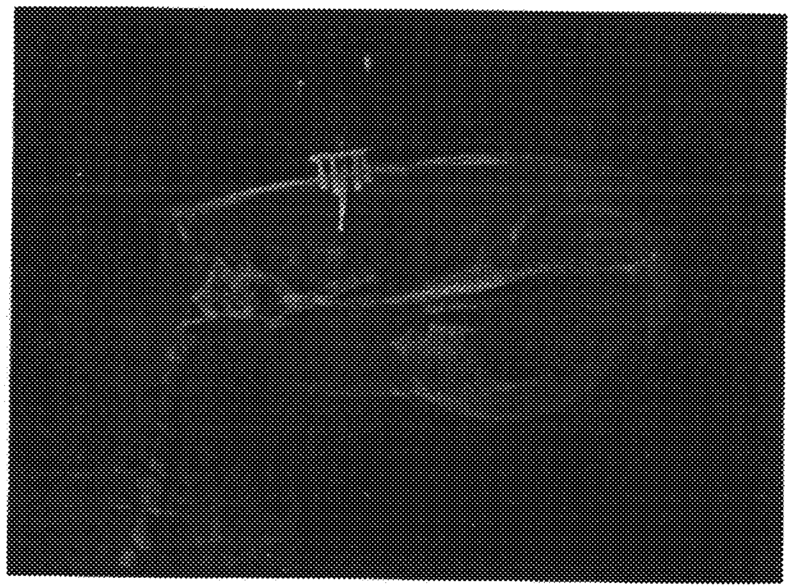

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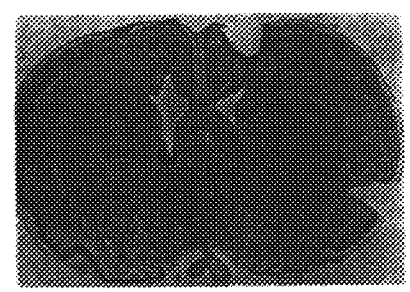

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If we move outside the septal area, either in the direction of the caudate nucleus (across the lateral ventricle) or in the direction of the *corpus callosum*, we find acquisition scores drop abruptly to levels of from 4 to 6 per

cent. These are definitely indications of neutral (neither rewarding nor punishing) effects.

However, above the *corpus callosum* in the cingulate cortex we find an acquisition score of 37 per cent. As the extinction score in this case was 9 per cent, we may say that stimulation was rewarding.

At the thalamic level (section II of Fig. 4) we find a 36 per cent acquisition score produced by an electrode placed again in the cingulate cortex, an 11 per cent score produced by an electrode placed in the hippocampus, a 71 per cent score produced by an electrode placed exactly in the mammillothalamic tract, and a zero per cent score produced by an electrode placed in the medial lemniscus. The zero denotes negative reinforcement.

At the mid-brain level (section III of Fig. 4) there are two zero scores produced by electrodes which are in the posterior portion of the medial geniculate bodies; here again, the scores indicate a negative effect, as the corresponding extinction scores are 31 and 21 per cent. There is an electrode deep in the medial, posterior tegmentum which produces a 2 per cent score; this seems quite neutral, as the extinction score in this case is 1 per cent.

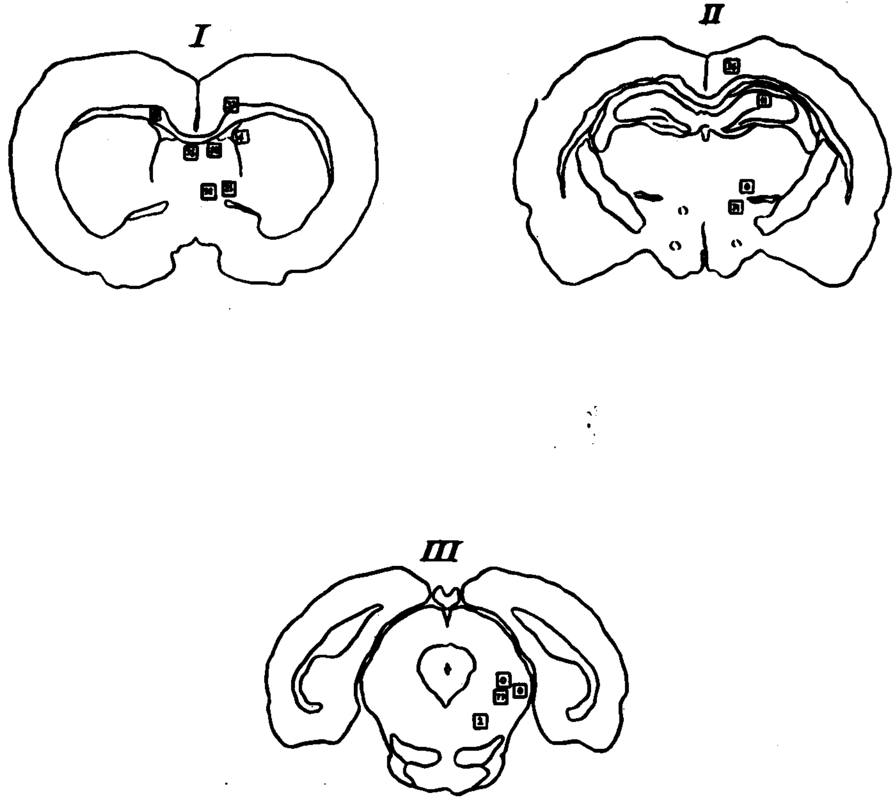

FIG. 4. Maps of three sections, (I) through the forebrain, (II) through the thalamus, (III) through the mid-brain of the rat. Boxed numbers give acquisition percentage scores produced by animals with electrodes stimulating at these points. On section I the acquisition scores 75, 88, 92, 85 fall in the septal forebrain area. On the same section there is a score of 4 in the caudate nucleus, a score of 6 in the white matter below the cortex, and a score of 37 in the medial (cingulate) cortex. On section II the acquisition score of 36 is in the medial (cingulate) cortex, 11 is in the hippocampus, 71 is in the mammillothalamic tract, and 0 is in the medial lemniscus. On section III the two zeroes are in the medial geniculate, 2 is in the tegmental reticular substance, 77 falls 2 mm. anterior to the section shown—it is between the posterior commissure and the red nucleus.

Finally, there is an electrode shown on this section which actually stands 1½ mm. anterior to the point where it is shown; it was between the red nucleus and the posterior commissure. It produced an acquisition score of 77 per cent, but an extinction score of 81 per cent. This must be a rewarding placement, but the high extinction score makes it difficult to interpret.

Behavior

We turn our attention briefly to the behavioral data produced by the more rewarding electrode placements.

The graph in Figure 5 is a smoothed cumulative response curve illustrating the rate of responding of rat No. 32 (the lowest-scoring septal area rat) during acquisition and extinction. The animal gave a total of slightly over 3000 responses in the 12 hr. of acquisition. When the current was turned on, the animal responded at a rate of 285 responses an hour; when the current was turned off, the rate fell close to zero.

The graph in Figure 6 gives similar data on rat No. 34 (the highest-scoring septal rat). The animal stimulated itself over 7500 times in 12 hr. Its average response rate during acquisition was 742 responses an hour; during extinction, practically zero.

Figure 7 presents an unsmoothed cumulative response curve for one day of responding

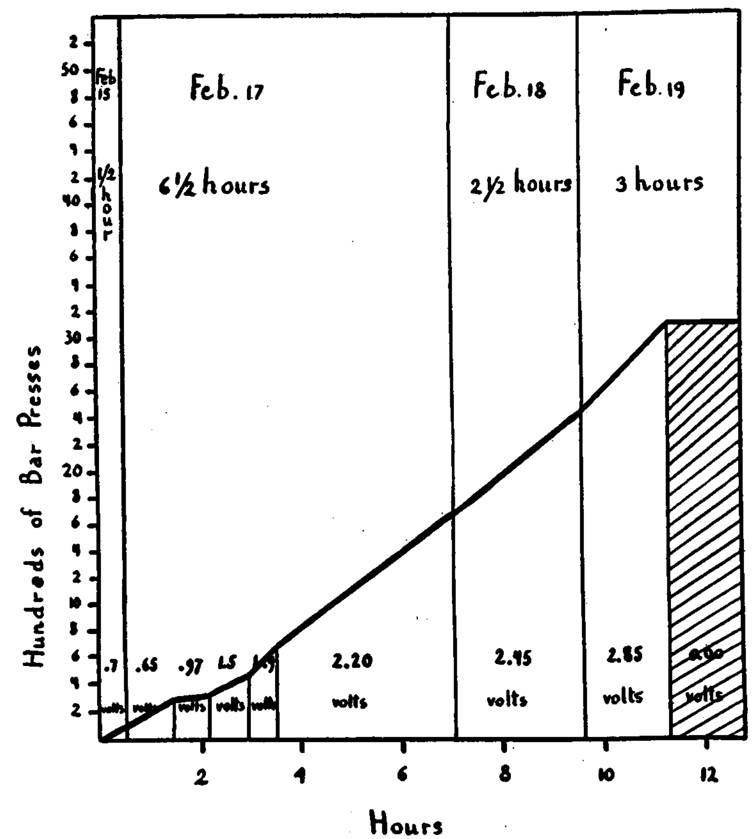

FIG. 5. Smoothed cumulative response curve for rat No. 32. Cumulative response totals are given along the ordinate, and hours along the abscissa. The steepness of the slope indicates the response rate. Stimulating voltages are given between black lines. Cross hatching indicates extinction.

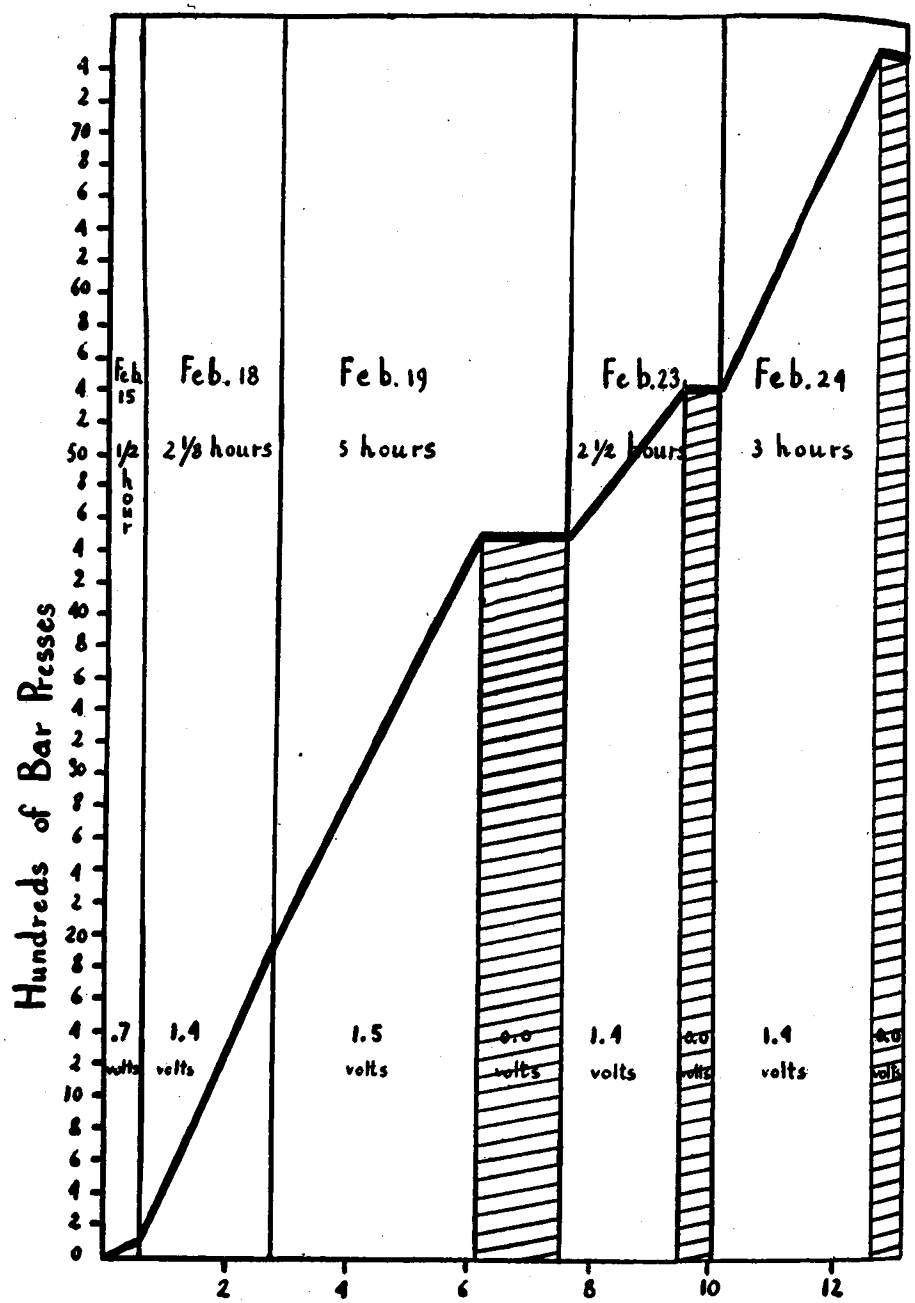

FIG. 6. Smoothed cumulative response curve for rat No. 34

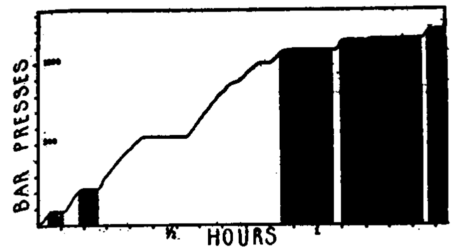

FIG. 7. Unsmoothed cumulative response curve showing about ¾ hr. of acquisition and ¾ hr. extinction for rat No. A-5. Shading indicates extinction.

for rat No. A-5. This is to illustrate in detail the degree of control exercised by the electrical reward stimulus. While this rat was actually bar pressing, it did so at 1920 responses an hour; that is, about one response for every 2 sec. During the first period of the day it responded regularly while on acquisition, extinguished very rapidly when the current was turned off, and reconditioned readily when the current was turned on again. At reconditioning points, *E* gave *S* one stimulus to show that the current was turned on again, but *E* did not place *S* on the lever. During longer periods of acquisition, *S* occasionally stopped responding for short periods, but in the long run *S* spent almost three-quarters of its acquisition time responding. During the long period of extinction at the end of the day, there was very little responding, but *S* could be brought back to the lever quite quickly if a stimulus was delivered to show that the current had been turned on again.

DISCUSSION

It is clear that electrical stimulation in certain parts of the brain, particularly the septal area, produces acquisition and extinction curves which compare favorably with those produced by a conventional primary reward. With other electrode placements, the stimulation appears to be neutral or punishing.

Because the rewarding effect has been produced maximally by electrical stimulation in the septal area, but also in lesser degrees in the mammillothalamic tract and cingulate cortex, we are led to speculate that a system of structures previously attributed to the rhinencephalon may provide the locus for the reward phenomenon. However, as localization studies which will map the whole brain with respect to the reward and punishment dimension are continuing, we will not discuss in detail the problem of locus. We will use the term "reinforcing structures" in further discussion as a general name for the septal area and other structures which produce the reward phenomenon.

To provide an adequate canvass of the possible explanations for the rewarding effect would require considerably more argument than could possibly fit within the confines of a research paper. We have decided, therefore, to rule out briefly the possibility that the implantation produces pain which is reduced by electrical stimulation of reinforcing structures, and to confine further discussion to suggestions of ways the phenomenon may provide a methodological basis for study of physiological mechanisms of reward.

The possibility that the implantation produces some painful "drive stimulus" which is alleviated by electrical stimulation of reinforcing structures does not comport with the facts which we have observed. If there were some chronic, painful drive state, it would be indicated by emotional signs in the animal's daily behavior. Our *S*s, from the first day after the operation, are normally quiet, nonaggressive; they eat regularly, sleep regularly, gain weight. There is no evidence in their behavior to support the postulation of chronic pain. Septal preparations which have lived healthy and normal lives for months after the operation have given excellent response rates.

As there is no evidence of a painful condition preceding the electrical stimulation, and as the animals are given free access to food and water at all times except while actually in the Skinner boxes, there is no explicitly manipulated drive to be reduced by electrical stimulation. Barring the possibility that stimulation of a reinforcing structure specifically inhibits the "residual drive" state of the animal, or the alternative possibility that the first electrical stimulus has noxious aftereffects which are reduced by a second one, we have some evidence here for a primary rewarding effect which is not associated with the reduction of a primary drive state. It is perhaps fair in a discussion to report the "clinical impression" of the *Es* that the phenomenon represents strong pursuit of a positive stimulus rather than escape from some negative condition.

Should the latter interpretation prove correct, we have perhaps located a system within the brain whose peculiar function is to produce a rewarding effect on behavior. The location of such a system puts us in a position to collect information that may lead to a decision among conflicting theories of reward. By physiological studies, for example, we may find that the reinforcing structures act selectively on sensory or motor areas of the cortex. This would have relevance to current S-S versus S-R controversies (8, 9, 13, 16).

Similarly, extirpation studies may show whether reinforcing structures have primarily a quieting or an activating effect on behavior; this would be relevant to activation versus negative feedback theories of reward (6, 13, 15, 17). A recent study by Brady and Nauta (1) already suggests that the septal area is a quieting system, for its surgical removal produced an extremely active animal.

Such examples, we believe, make it reasonable to hope that the methodology reported here should have important consequences for physiological studies of mechanisms of reward.

SUMMARY

A preliminary study was made of rewarding effects produced by electrical stimulation of certain areas of the brain. In all cases rats were used and stimulation was by 60-cycle alternating current with voltages ranging from ½ to 5 v. Bipolar needle electrodes were permanently implanted at various points in the brain. Animals were tested in Skinner boxes where they could stimulate themselves by pressing a lever. They received no other reward than the electrical stimulus in the course of the experiments. The primary findings may be listed as follows: (*a*) There are numerous places in the lower centers of the brain where electrical stimulation is rewarding in the sense that the experimental animal will stimulate itself in these places frequently and regularly for long periods of time if permitted to do so. (*b*) It is possible to obtain these results from as far back as the tegmentum, and as far forward as the septal area; from as far down as the subthalamus, and as far up as the cingulate gyrus of the cortex. (*c*) There are also sites in the lower centers where the effect is just the opposite: animals do everything possible to avoid stimulation. And there are neutral sites: animals do nothing to obtain or to avoid stimulation. (*d*) The reward results are obtained more dependably with electrode placements in some areas than others, the septal area being the most dependable to date. (*e*) In septal area preparations, the control exercised over the animal's behavior by means of this reward is extreme, possibly exceeding that exercised by any other reward previously used in animal experimentation.

The possibility that the reward results depended on some chronic painful consequences of the implantation operation was ruled out on the evidence that no physiological or behavioral signs of such pain could be found. The phenomenon was discussed as possibly laying a methodological foundation for a physiological study of the mechanisms of reward.

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Received July 15, 1954.