1967

A study of relations between intracranial self-stimulation and operant behavior maintained by food reward

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A Study of Relations Between Intracranial Self-Stimulation

and Operant Behavior Maintained by Food Reward

A Thesis Presented

by

Jaak Panksepp

Submitted to the Graduate School of the
University of Massachusetts in
partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

September, 1967

Major Subject: Psychology

Abstract

In the present investigation a series of experiments was
run in an attempt to simulate one aspect of food based behavior,
satiation, during self-stimulation, and to replicate behavior pec-
uliar to the self-stimulation situation with a food reward.

For the first experiment a swivel was developed for concurrent
intraorganismic fluid injection and intracranial electrical stimula-
tion of the unrestrained rat. Using this swivel, the effect of various
intragastric injections on self-stimulation of the lateral hypothalamus
was studied. In some subjects intragastric injections of both water
and milk decrease self-stimulation. This decrease was reflected by
pauses in self-stimulation rather than by an overall decrease in the
rate of responding. In other subjects, however, neither injections
of water nor nutritive solutions affected the rate of self-stimulation.

In the second series of experiments the behavior of rats prepared
with chronic mouth fistulas working for an intraorally administered
reward was compared to animals receiving the same food reward in a
conventional manner. The behavior of the fistulated animals was strik-
ingly similar to the behavior of animals responding for rewarding
electrical stimulation of the brain. Evidence for fast acquisition,
fast extinction, priming, and extinction without responding is reported.
Self-stimulation data was best simulated by intraoral self-injection
animals on an ad libitum food schedule, whose behavior was maintained
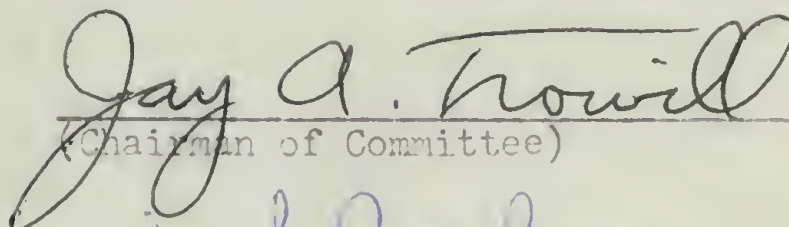by the incentive quality of the food reward.

A STUDY OF RELATIONS BETWEEN INTRACRANIAL SELF-STIMULATION

AND OPERANT BEHAVIOR MAINTAINED BY FOOD REWARD

A Thesis Presented
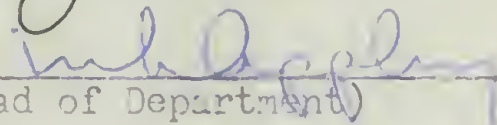
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Jaak Panksepp

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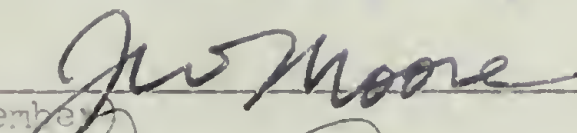
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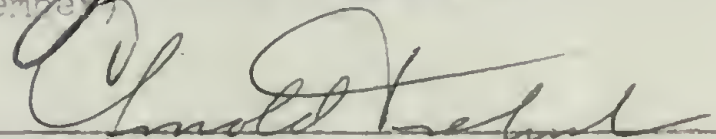
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September, 1967

Acknowledgements

The author wishes to thank the members of his thesis committee, Dr. Jay A. Trowill, Dr. John Moore, and Dr. Arnold Trehub, for their cooperation in the completion of this research. I am particularly grateful to Dr. Jay A. Trowill for his encouragement and advice throughout each phase of this study, and to Dr. Arnold Trehub who lent the use of his facilities for the completion of the first experiment in this study.

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General Introduction

Since the demonstration of the intracranial self-stimulation
phenomenon by Olds and Milner (1954), it has not been clearly deter-
mined whether such brain stimulation is comparable to other primary
rewards for controlling behavior. Presently all that can be said
is that behavior maintained by electrical stimulation of the brain
(ESB) is similar in some respects to behavior maintained by conven-
tional reinforcers and seemingly different in others (Grossman, 1967;
Gallistel, 1964; Zeigler, 1957).

Major similarities have been found in experiments where the
mode of responding has been measured under various schedules of
reinforcement. Sidman, Brady, Conrad and Schulman (1955) demonstra-
ted that the character of responding for ESB under a FR-8 or VI-16
sec. schedule was similar to that found with food reinforcement.
Self-stimulation lore still maintained, however, that animals would
only maintain responding on relatively easy schedules of reinforcement
(Gallistel, 1964). Pliskoff, Wirght and Hawkins (1965) were, however,
able to establish schedules of reinforcement with ESB as reward that
were comparable to those used with conventional reinforcers. They
did this by using a situation where pressing a permanent lever under
various intermittent schedules produced a retractable lever upon
which ESB was available on a CRF schedule. In such a manner the
following schedules of reinforcement on the permanent lever were
maintained: FI-30 min, FR-200, VI-4 min, and DRL-3 min.

Although Pliskoff, et al. (1965) were able to get DRL schedules
with the two bar chaining situation, it is interesting that under
certain conditions DRL schedules have not been obtained with
conventional rewards. Conrad, Sidman and Herrnstein (1958) showed
that animals were able to withold a response according to a DRL
schedule across a wide range of food deprivation conditions, but
animals tested at a low level of food deprivation did not learn to
wait sufficiently long before responding under DRL schedules. This
suggests why it is difficult to get animals to respond for ESB on
DRL schedules in the conventional one bar situation (Brady and Conrad,
1960). The ability to obtain DRL schedules with both food and ESB
reward may thus be dependent on an appropriate drive being present.

Similarities between behavior maintained by ESB and conventional
reinforcers have also been found in discrete trial situations. Olds
(1956) demonstrated that there were no differences in acquisition or
extinction between ESB and food rewarded animals when running speed
in a maze was the dependent measure. One difference between ESB and
food reinforced groups did appear, however. Whereas the food group
showed improved performance on the first trial of each succeeding
day, the ESB rewarded animals showed a slower running speed on the
first trial compared to the last trial of the previous day.

Most of the reported dissimilarities between the two rewards
are derived from free-operant situations. Using such procedures it
has been demonstrated that ESB motivated behavior produces more rapid
acquisition (Olds, 1956), and more rapid extinction (Seward, Uyeda and

Olds, 1959; Culbertson, Kling and Berkley, 1966), than food reinforced behavior, agitation and excitement in responding (Grover, 1960), and the absence of a conditioned emotional response under conditions where one is normally elicited during food rewarded testing (Brady, 1957). Other dissimilar characteristics that have been cited are the lack of satiation of ESB (Olds, 1958), the motivation inducing effect of non-contingent priming stimulations (Olds and Milner, 1954), and extinction in the absence of responding (Howarth and Deutsch, 1962).

It is the opinion of several researchers (Pliskoff, et al., 1965) that even these differences will be eliminated once certain uncontrolled variables are accounted for. Already Herberg (1963, 1965) has presented evidence for the conclusion that the rapid extinction of ESB in free-operant situations reflects characteristics of the reinforcement schedule rather than any peculiarity of ESB itself. He showed that the rapid extinction demonstrated with ESB was partially a training effect produced by the long, unvarying series of stimulations typical of a normal self-stimulation session. Herberg maintains that the rapid extinction is due to an overtraining effect. He points out that a decrease in resistance to extinction with overtraining has been demonstrated with conventional rewards in the runway, after partial (Capaldi, 1958) and continuous (North and Stimmel, 1960; Ison and Cook, 1964) reinforcement. The same effect has sometimes been produced in free operant situations (King, Wood and Butcher, 1961), but not at other times (Margulies, 1961; D'Amato, Schiff and

Jagoda, 1962). Herberg also showed that groups of animals equated for total number of reinforcements, but given a different number of extinction sessions differed in resistance to extinction. The more extinction an animal had experienced, the faster it extinguished in subsequent sessions. Herberg points out that this is similar to the process of conditioned inhibition that has been demonstrated with conventional rewards.

There is still uncertainty whether secondary reinforcement can be demonstrated using ESB as the primary reinforcer. Stein (1958) demonstrated that after pairing a tone with administration of ESB in a classical conditioning paradigm, the tone possessed reinforcing properties. Seward, et al. (1959), however, failed to demonstrate secondary reinforcement with a light that had been paired with ESB in a free-operant situation. Mogenson (1965), in replications of both the Stein and Seward procedures, was unable to find a secondary reinforcement effect with either of them. Recently it has been demonstrated that the secondary reinforcement can be demonstrated with ESB but that an appropriate drive has to be present during training. DiCara (1966) has shown that for lateral hypothalamic placements an appropriate drive was food but not water deprivation. More recently Hynek (1967) has presented some evidence that secondary reinforcement can be demonstrated in the U-maze situation with freely fed animals.

In an attempt to reconcile some of the disparities found between ESB and food reinforced behavior two experiments were run. The first

experiment attempted to establish a satiation effect such as is
found with food and water ingestion during a self-stimulation session.
This was done by superimposing various intragastric injections on
ESB maintained bar pressing. The second experiment attempted to
simulate characteristic ESB based behavior (rapid acquisition, fast
extinction, priming effects and extinction in the absence of responding)
in a free operant situation with a food reinforcer.

Study I

A Study of Negative Feedback Control

of Self-stimulation

The maintenance of responding by electrical stimulation of the
lateral hypothalamus has been viewed as a positive feedback system
because of the lack of satiation for this stimulation (Olds, 1958).
This statement is incorrect to the extent that the lack of satiation
may demonstrate either a positive feedbak system or the lack of any
operating feedback system at all. Regardless of which it is, stimu-
lation of the lateral hypothalamus has the ability to abolish the
regulation of other control systems. For instance Routtenberg and
Lindy (1965) and Spies (1965) demonstrated that rats permitted to
self-stimulate during their daily feeding session preferred to self-
stimulate, and in effect, self-starved. This effect , however,
was shown to be a function of the brain location being stimulated.
Brady (1958), on the other hand, has demonstrated that for certain
septal electrodes, self-stimulation occurs only under conditions of
water deprivation and disappears precipitously with water satiation.
Here it seems that some effect of water ingestion has a negative
feedback control over self-stimulation. Although such striking
"satiation" effects have not been demonstrated at other sites, many
experiments have demonstrated that rates of self-stimulation from
various brain sites is correlated with the presence of specific
drives—the higher the drive, the higher the rate of self-stimulation.

Olds (1962) has reviewed studies showing a correlation between drive states and self-stimulation. It has been demonstrated that the rate of responding for ESB from certain hypothalamic electrode placements has covaried with the level of food deprivation (Olds, 1958; Hodos & Valenstein, 1960), the level of circulating androgens in the male rat (Olds, 1958) and the estrous cycle of the female rat (Prescott, 1966). The immediacy of the decline in rate of responding by food deprived rats with lateral hypothalamic placements was demonstrated by Hoebel and Teitelbaum (1962) by interpolating tube feeding of deprived subjects within a single testing session.

A suggestion of how this decrement in responding for ESB occurs in animals at a low level of food deprivation is implicit in Anand and Brobeck's (1951) proposed satiety mechanism. Anand and Brobeck proposed that satiety increased activity in the ventromedial nucleus of the hypothalamus (VMN) which then inhibited activity of certain lateral hypothalamic areas. Hoebel and Teitelbaum (1962) found that an immediate increase in the rate of lateral hypothalamic self-stimulation ensued when the VMN was anesthetized. Hence they proposed that the decreased responding of satiated rats resulted from inhibition of lateral hypothalamic self-stimulation. Since then, Anand and his colleagues (Anand, Dua and Singh, 1961; Anand, Chhina and Singh, 1962; Anand, Chhina, Sharma, Dua and Singh, 1964) have presented electrophysiological evidence of a direct relationship between VMN activity and hyperglycemia, and lateral hypothalamic activity and hypoglycemia; and

of a inverse relationship between VMN activity and hypoglycemia,
and lateral hypothalamic activity and hyperglycemia. Oomura,
Kimura, Ooyama, Maeno, Iki and Kuniyoshi (1964) and Oomura, Ooyama,
Yamamoto and Naka (1967) have demonstrated the reciprocal relation-
ship between spontaneous unit discharges between the VMN and lateral
hypothalamus. Furthermore Szentágothai, Flerkó, Mess and Harlász
(1962) have described extremely fine caliber neuronal connections
between the VMN and lateral hypothalamus.

Since it has been demonstrated that postingestional consequences
of food intake have a negative feedback control over lateral hypo-
thalamic activity, the following experiment was devised to test
whether the intragastric administration of various solutions during
self-stimulation would produce satiation for lateral hypothalamic
self-stimulation. To run this experiment, a swivel and animal
coupling system was developed for concurrent brain stimulation and
intraorganismic fluid injection in the unrestrained rat.

Method

Subjects--Four experimentally naive 120 day old Sprague Dawley male
rats wighing 280-330 grams were implanted with chronic intragastric
fistulas (see Appendix B). During the same operation, commercial
bipolar stainless steel electrodes (.018 in. tip diameter) insulated
throughout except at the tips, aimed at the lateral hypothalamus,

were implanted. The stereotaxic coordinates (deGroot, 1959) were
as follows: Rat 1: A-4.6, L-1.5, H-3.0; Rat 2: A-5.8, L-1.7,
H-2.5; Rat 3: A-4.8, L-1.9, H-3.0; Rat 4: A-5.0, L-1.8, H-3.0.
After five days of post-operative recovery all rats except Rat 3
were placed on a daily 22 hr. food deprivation schedule for approx-
imately one week prior to experimentation and continuing for the
duration of the experiment. During experimentation a two hour
feeding period was allowed immediately after the test session. Rat
3 was maintained on free-feeding thoughout the experiment. Water
was available in the home cages at all times, except before Session
3, when Rats 1 and 2 were deprived of water for six hours.

Procedure--A single lever operant conditioning box used in conjunction
with conventional programming and recording devices served as the
experimental apparatus. During the first session, each rat was trained
to lever press on a CRF schedule for ESB. After learning the response,
the subjects were allowed to respond for 45 min. Each reinforcement
consisted of a 0.3 sec train of 60-pulse/sec, biphasic, 0.1-msec
pulses from a Grass S-4 stimulator. The stimulation voltage was
continuously monitored on a cathode ray oscilloscope. Current inten-
sities were initially chosen for each rat so as to sustain responding.
These currents were used in subsequent sessions. The intensities used
were 70 μA, 80 μA, 76 μA and 120 μA (all currents are zero to peak)
for Rats 1 through 4 respectively. Each successive testing session
was separated by a day. During Session 2 each rat was allowed to

self-stimulate on a CRF schedule without intragastric injection
for one hour. During Session 3 Rats 1 and 2 were allowed to self-
stimulate on a CRF schedule; superimposed on the CRF responding for
ESB, intragastric injections of water were given on a fixed ratio 5
(FR-5) schedule. For Rats 3 and 4, instead of water, a commercial
milk solution (undiluted Metrecal) and a 32 % (32 g sucrose mixed
in enough water to make 100 ml of solution) sucrose solution were
injected, respectively. Rats 1 and 2 were given an additional
session during which the Metrecal milk solution was injected on a
FR-5 superimposed on the CRF responding for ESB. The individual
injections consisted of .065 $\pm$ .005 ml of fluid. The nutrient
density of the milk injections was 0.92 Cal/ml and that of the
sucrose solution, 1.28 Cal/ml.

Results

Figure 1 consists of the cumulative records of Rats 1, 2 and 4.
Two characteristic types of responding were found from the sites
studied. Two rats showed some form of modulation of self-stimulation
due to the intragastric injections and two did not.

Rats 1 and 4 showed little modulation of responding as a result
of either the intragastric water, milk or sucrose injections. The
self-stimulation session for Rat 1 was terminated when the quantity
of injected fluid had greatly exceeded what had previously been
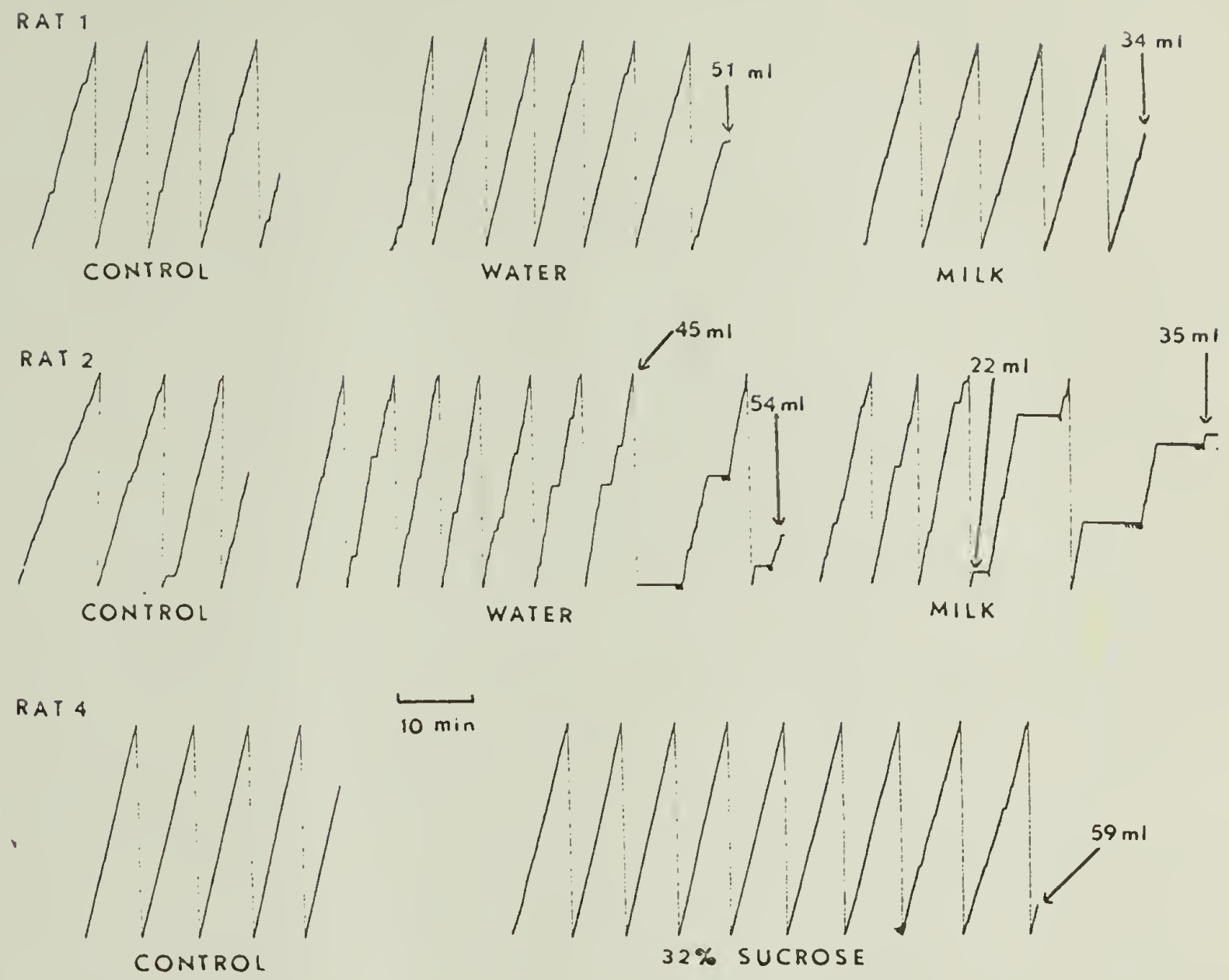
Fig. 1. Cumulative records for sessions 2-4 for Rats 1 and 2, and for
sessions 2 and 3 for Rat 4. The records of the control sessions
represent only the second half of a hour long self-stimulation
session. Each record is labeled with the treatment administered
during that session and the terminal injected fluid volumes for
all subjects. For Rat 2 the injected volume at the first
protracted termination of responding is given. The downstrokes
on the records of Rat 2 represent non-contingent brain stimula-
tions. Each excursion of the cumulative recorder pen represents
550 bar-presses.

reported (Hoebel and Teitelbaum, 1962) to have produced inhibition
of self-stimulation. Since neither a 51 ml stomach load of water,
nor a 34 ml load of milk produced inhibition of self-stimulation,
it was concluded that the intragastric injections were not modulating
self-stimulation at this hypothalamic site. For Rat 4 the sucrose injec-
tion session was extended to see if self-stimulation would terminate
with an extreme intragastric load of a nutritive substance. The
subject was still self-stimulating when the stomach load had reached
59 ml. This represented a weight increase of 21% over pre-session
weight. Since there was no apparent change in overall response rate
in spite of the increasing deleterious effects of this large gastric
load, the session was terminated with the hope of preserving the
animal. The rat was extremely bloated, and the abdominal skin was
expanded tautly. The next morning the animal was found dead in its
cage. The abdominal cavity was opened and the gut was found to be
engorged with fluid. It is possible that death resulted from dehy-
dration due to the hypertonic sucrose solution drawing water from the
tissues and extracellular fluid into the gastrointestinal cavities.

Rats 2 and 3 demonstrated a pattern of responding that was
noticeably affected by the injection procedures. Since the cumulative
records of Rat 3 were topographically similar to the corresponding
records of Rat 2, they have not been included in Fig. 1. Both the
water and milk injections decreased the amount of self-stimulation
during the later part of the sessions as can be seen for Rat 2 in
Fig. 1. For both animals this decrease was a result of terminations
of responding rather than an overall decrease in the rate of responding.

The first protracted (at least 2 min.) termination of responding for Rat 2 during the water injection session occurred at a stomach load of 45 ml, but with the milk injection, the first termination occurred at a load of 22 ml. For Rat 3, who had been maintained on free feeding, the first termination during milk injections occurred at a load of 9 ml. When such terminations of responding had lasted for at least 2 min, non-contingent stimulations were administered to bring the subjects back to the bar. Responding resumed with these administrations during both water and milk injection sessions, but subsequent terminations occurred at increasingly shorter intervals.

During the control sessions Rats 1 and 4 could be differentiated from Rats 2 and 3 by their predominant mode of responding. The main behavior pattern of Rats 2 and 3 was vigorous biting of the bar, while Rats 1 and 4 responded primarily with their front paws and exhibited few oral responses. Furthermore, though Rats 1 and 4 exhibited no decrease in overall responding, they did show increasingly erratic responding during the later parts of the injections sessions, but Rats 2 and 3 actively avoided the bar by going to the other end of the training chamber and crouching.

Histological verification of electrode locations was not accomplished because animals died from antibiotic reactions post-experimentally. The high control rates of self-stimulation, however, are comparable to those usually found with lateral hypothalamic placements.

Discussion

The data demonstrated the ability of both food and water to bring responding for ESB from certain hypothalamic sites under the control of intragastric injections. That this control commenced sooner for the milk injected animals than for the water injected one, and for the free-fed animal before the deprived animal, shows that some quality of the nutritive solution was crucial to the early cessation of responding. Presently it can not be determined what postingestional factor caused this effect.

It is interesting that those areas that were sensitive to milk injections were also eventually sensitive to water injection. The sensitivity of self-stimulation to nutritive injections can be explained by increased VMN activity and its subsequent inhibition of certain lateral hypothalamic areas (Anand, et al., 1961, 1962, 1964). It is possible that the inhibition due to water injections resulted from stomach distention, mediated by the afferent gastric receptors described by Paintal (1954). The potent effect of stomach distention on increasing VMN activity has been demonstrated by Sharma, Anand, Dua and Singh (1961). Hence both a chemical quality of the food and the bulk of the food can increase the activity of the VMN. The slower inhibition of self-stimulation resulting from non-nutritive stomach injections is due to the slow buildup of stomach distention to a value sufficient to change the activity of the VMN.

Hoebel and Teitelbum (1962) reported both animals in which the interpolated intragastric injection of milk decreased lever pressing

rate relatively uniformly and those in which responding rate was
maintained but interrupted repeatedly by other activities such as
grooming. Rats 2 and 3 exhibited the second type of response
modulation, periods of cessation of responding, but rather than
indulging in extraneous behavior during these pauses they would
actively orient away from the bar. Then, however, responding was
reinstated by administration of noncontingent reinforcements, the
pre-stopping rate was again resumed. Hence, in the animals used here,
the intragastric injections did not modulate the rate of responding
but did modulate the duration and frequency of bouts of responding.
In this sense, it is similar to other response measures such as rate
of licking (Hill and Stellar, 1951; Davenport, 1961; Stricker and
Miller, 1965) which does not vary with level of thirst until pauses
occur with satiation late in the session.

The inability of intragastric injections to assume control
over self-stimulation from some hypothalamic sites was also demonstrated.
Rat 1 received large amounts of both food and water with no concurrent
decrement in responding. Rat 4 exhibited a striking maintenance of
performance despite an enormous and probably painful hypertonic stomach
load. The maintenance of self-stimulation under conditions that upset
body fluid balance beyond physiological limits demonstrates the potency
of ESB either as a very strong reinforcer of ongoing behavior, or as a
stimulus that has the ability to increase the pain threshold of an
animal. It is probable that rewarding ESB has both properties. This

(1961) and Valenstein and Beer (1962) demonstrated that a rat will
accept intense footshock to obtain ESB. Furthermore, Heath (1954),
Andy (1958), Lilly (1960) and Cox and Valenstein (1965) have reported
that self-stimulation at certain sites does increase the pain
threshold of an animal. More recently Ball (1967) has demonstrated
that stimulation of brain loci that support self-stimulation inhibits
sensory input into the trigeminal nucleus.

Two further explanations for the enormous intake of Rats 1
and 4 could be posited. A stimulus bound eating "center" (Miller,
1960) may have been located under the stimulating electrode. Such
stimulation would have the capacity to increase intake above normal
limits. The last possibility is that the neural consequences of the
stomach injections did not acquire functional connections with the
positive reinforcing system being stimulated. Hence the consequences
of the intragastric injections may not be able to modulate the quality
of the ESB nor the response system that is being activated by the ESB.
Support for such a possibility has been presented by Hodos and Valen-
stein, (1960) who noted that a relationship between drive level and
self-stimulation has not been consistently found from some hypothalamic
locations.

Study II

The Simulation of Intracranial Self-Stimulation

Based Behavior with a Food Reward

Experiment I

Effect of Delay of Reward on Acquisition

and Extinction

It has been pointed out that performance measures from instrumental learning situations using conventional reinforcers cannot be adequately compared with situations using rewarding ESB unless the temporo-spatial relation between response and reinforcement is equated (Gibson, Reid, Sakai and Porter, 1965). Specifically, in free operant bar-pressing situations using ESB, the reward is usually simultaneous with the response. With conventional rewards, however, the bar-press activates a dispensing mechanism and the animal has to make a chain of approach and consumatory responses before the reward is obtained. When the temporo-spatial relations are made similar by either prolonging the response-reinforcement delay in the ESB free-operant situation to delays typical of conventional free-operant learing situations (Gibson, et al., 1965) or by using discrete trial situations such as the runway (Olds, 1956), acquisition and extinction data are comparable for the two rewards.

It has not yet, however, been adequately demonstrated that the behavior controlled by the two types of reinforcement are similar when the contingencies of the conventional reward situation are made identical with those of the normal ESB situation. One study (Gibson, et al.,

1965) has reported an attempt to shorten the latency of food reward
presentation to match that of the ESB situation. In that study, rats
received sugar water or ESB immediately upon licking a liquid dipper.
Both the animals rewarded with sugar water and those rewarded with
ESB extinguished in the same number of trials. However, since the
food reinforcement was delivered in the same dipper where the response
occurred, it is possible that the animals working for sugar water were
not required to make a true instrumental response. Licking, the
unconditioned response in the presence of the liquid reinforcement,
may have been sufficient to maintain the continued administration of
the reward. Hence the fast extinction exhibited by this group could
merely have been the decrease of the unconditioned response in the
absence of the appropriate consumatory object. Since the similarly
rapid extinction of ESB behavior may suggest that bar-pressing for
ESB is more like an unconditioned response than an instrumental
response, it is necessary to test whether the low resistance to
extinction occurs if the response-reinforcement contingency is main-
tained, but the response is changed to one of a clearly instrumental
nature--a bar-press. In this experiment an attempt was made to duplicate
some of the properties common to ESB based behavior in rats using natural
drive and reinforcement variables in a response-reinforcement contingent
free-operant ESB paradigm.

Subjects were prepared with chronic mouth fistulae (see Appendix B)
such that a highly palatable reinforcement solution could be delivered
directly into the mouth with a minimum of delay. The nature of this

preparation precluded the chain of sensory interaction with the reward object preceding ingestion, and is thus a close approximation to ESB administration. The effects of immediate intraoral administration of reward were studied in terms of acquisition and extinction and other performance variables.

Method

Subjects--Twenty male albino rats weighing 250-350 g. were randomly assigned to five experimental conditions, four to a group. Three groups were implanted with chronic mouth fistulae (see Appendix B), and the other two groups were unoperated controls. Subjects were maintained on a 23 hour food deprivation schedule for at least one week before the operation and for one week between the operation and the initiation of training. During the experiment, subjects were maintained on a $23\frac{1}{2}$ hr food deprivation schedule.

Apparatus--A single lever operant conditioning box $9\frac{3}{8}$ by 8 by $7\frac{1}{2}$ in. with a Lehigh Valley liquid dipper mounted 2 in. to the left of the bar served as the experimental chamber. A circuit for sensing contacts was attached to the dipper. The apparatus for self-injection of fluids in a free-operant situation was the same as used in the previous experiment (see Appendix A). The reinforcement used for all groups, a commercially prepared chocolate milk, has proved to be a food of high incentive value for rats whether administered intraorally or by dipper. Each reinforcement was .04 ml in volume.

Procedure--Experimental conditions differed in the method of administration of reward and in the delay of reward. For three groups,

reinforcement was available at the dipper. For one of these groups, designated as D-D (dipper-delay), a bar press activated the dipper mechanism. For the second group, D-I (dipper-immediate), touching the liquid cup of the dipper activated the dipper mechanism and made food available for two sec. before the touch sensor was reactivated to allow another lick to activate the dipper. For the third group, O-C (oral-chained), a bar press armed the dipper touch sensor, and the animals contact with the dipper caused the liquid reinforcement to be injected intraorally. Because of a leak in one of the animal's fistual, data was collected from only three animals in this group.

For the other two groups, the liquid reinforcement was also dispensed directly into the mouth. For one group, O-I (oral-immediate), the injection was contiguous with the bar press. For the other group, O-D (oral-delay), the injection was administered 3.3 sec after the bar-press. This delay represented a mean value based on the delay of ingestion of group D-D. Since a retractable bar was not used, group O-D responded in effect as a low variable-ratio group.

All animals were given a day of training and three days for stabilization of the response. During each of these sessions, the subjects were allowed 100 reinforcements. On day 5, 50 rewards were given followed by a 30 min extinction session. On the third day after extinction, all animals were given a 15 min session to test for spontaneous recovery. The number of shaping trials necessary to lead to acquisition (i.e., sustained responding in the situation) was

measured for subjects in groups O-I and D-D, and the number of responses per minute was recorded during training, extinction and spontaneous recovery for all groups.

Results and Discussion

The animals in the O-I group showed remarkably fast acquisition. All O-I animals were trained in between 1 and 3.5 min with a maximum of 21 shaping reinforcements ($\bar{x}$ = 2.5 min, 15 reinforcements). D-D animals required between 18 and 35 min of shaping during which time 63 to 80 reinforcements were administered. Both of these differences were significant by the Mann-Whitney U test[1], (U = 0, p < .014).

Since a short response-reinforcement delay has been asserted to lead to fast extinction (Gibson, et al., 1965), it would be expected that group O-I should show less resistance to extinction than group D-D. The extinction data (Fig. 2 and Table 1) failed to confirm this prediction. Statistical tests show that there was no significant difference (p > .343) between these groups. Group D-I, however, did have significantly (p < .024) less resistance to extinction than any of the other groups. This effect, which has been previously been reported (Gibson, et. al., 1965), has been the basis for maintaining that there are not differences in resistance to extinction between

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1. The statistical test used for all comparisons in this experiment was the Mann-Whitney U-test.
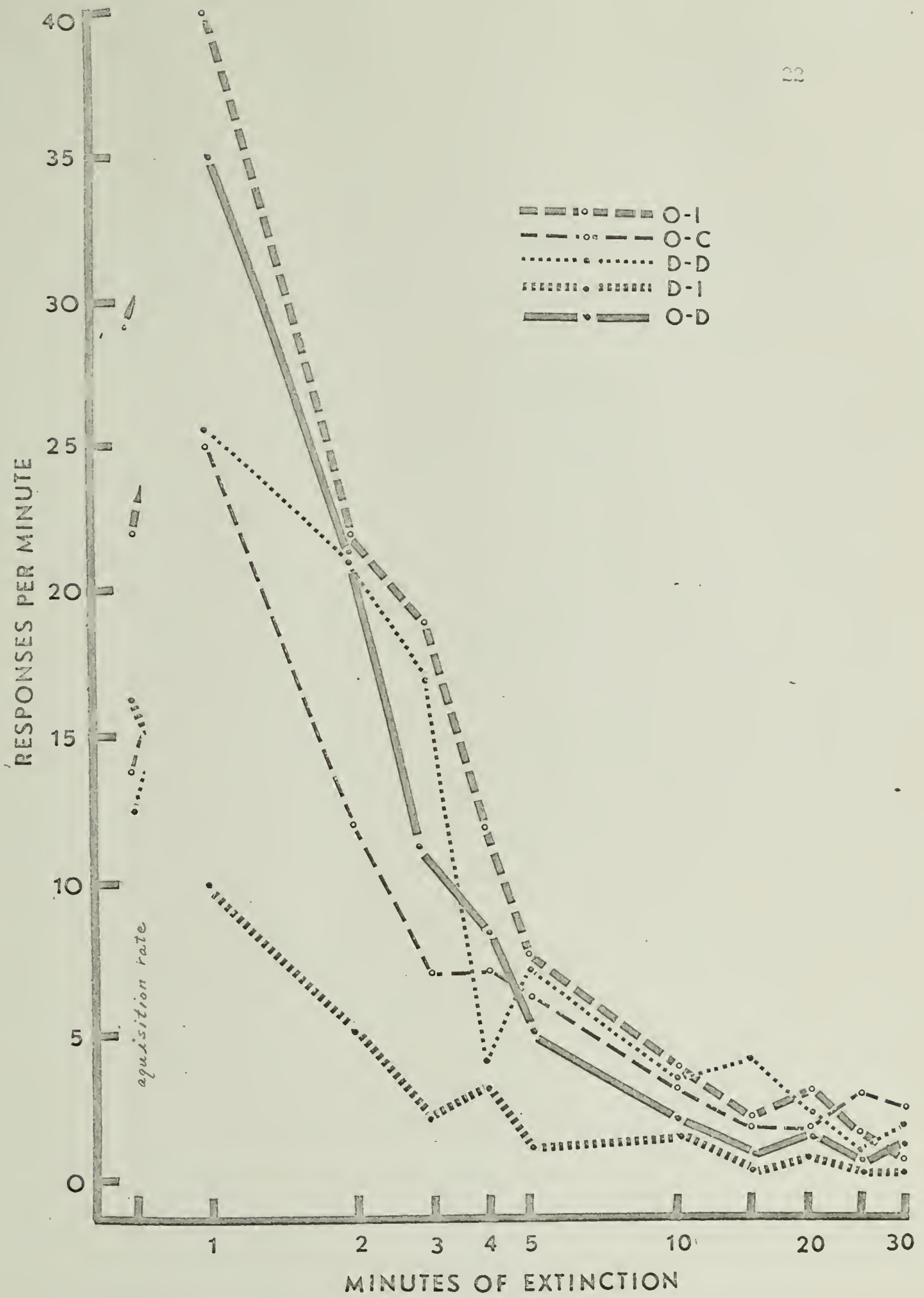
Fig. 2. Response rates during extinction compared with rates during reinforcement. Responses are represented by 1-minute means on the left and by 5-minute means on the right.

Table 1.   Number of responses per subject and group means for the
30 minute extinction session of Experiment I.

Extinction Scores

S's   Groups

		D-D	D-I	O-C	O-I	O-D
1		157	53	105	109	147
2		124	42	173	124	136
3		109	24	77	110	96
4		137	17	**	250	65
	X	527	136	355	593	444
	X̄	132	34	118	148	111

Spontaneous Recovery

		D-D	D-I	O-C	O-I	O-D
1		*	7	20	24	14
2		32	5	22	38	12
3		24	6	5	9	54
4		12	3	**	19	*
	X	68	21	47	90	80
	X̄	23	5	16	22	27

** Animal not tested due to leaky fistula
* Animals pulled caps

ESB and conventional rewards once the delay of reward has been
equated. The present data, however, shows that the same low
resistance to extinction did not occur in group O-I, a group where
the reward was also delivered immediately.

It is striking that there were no significant differences
(p's > .100) in resistance to extinction among groups D-D, O-I, O-C,
and O-D. A difference between O-I and O-D animals may have been
expected from a delay of reinforcement effect. It has been demon-
strated that increasing delay of reinforcement increases resistance
to extinction in the runway situation (Ferrer, 1956; Peterson, 1956;
Sgro and Weinstock, 1963); however, no adequate demonstration of this
effect is available for the free operant situation. The present
data, however, is not well suited for drawing conclusions about
a delay of reinforcement effect in a free operant situation since
the delay for group O-D was confounded by the responses made on the
bar during the delay. It would still be expected that O-D animals
would show greater resistance to extinction from a partial reinforce-
ment prediction. The group O-D mean response rate during extinction
tended, however, to be lower than that of the O-I group--an effect
contrary to a PRE prediction. The reason a PR effect did not occur
in the O-D animals may be due to some unique factor of the intraoral
injection procedure in a free operant situation. Possibly, the reward
during acquisition was such an integral part of the stimulus complex
that elicited the response (food ⟶ chewing the bar) that the O-D

subjects hardly differentiated the low VR schedule they were res-
ponding on from the CRF schedule that the O-I subjects were under.
This hypothesis could be tested by making the instrumental response
such as to preclude any oral response on the manipulandum. Possibly,
panel pushing would be such a response.

Responding during the spontaneous recovery session was
significantly greater (p < .028) for groups O-I, O-D and D-D than
for group D-I. Groups O-I, O-C, O-D and D-D did not, however, differ
significantly from each other (p > .300). The low spontaneous recovery
and extinction score of group D-I suggests that licking the liquid
dipper was not a true instrumental response in this situation.
Furthermore, the fact that O-I animals were at least as resistant
to extinction as D-D animals suggests that delay of reinforcement
alone is not the crucial variable that produces fast extinction in
the free-operant FSB situation.

Experiment II

Drive Level as a Determinant of Extinction Responding

and

Experiment III

A Test for Extinction Without Responding with a Conventional Reward

Although there was no indication of rapid extinction in group
O-I, it should be noted that the animals were maintained at a high
level of food deprivation. Recent evidence suggests that animals res-
ponding for ESB to certain locations have greater resistance to extinc-
tion if tested at a high drive level (Deutsch and DiCara, 1967). The
more cogent comparison to normal ad lib ESB animals may thus be an
O-I group maintained on free feeding whose responding is maintained
by the incentive quality of a food reward. The following experiments
were run to compare the resistance to extinction between animals
maintained on an ad lib feeding schedule and those maintained on a
23 hr food deprivation schedule, and to test whether extinction without
responding could be obtained with a conventional reward.

Method

Eight of the fistulated animals used in the previous experiment
were randomly divided into two groups. Four animals were put on a
23 hr deprivation schedule (group-DEP), and the other 4 were allowed
food ad libitum (group-AD LIB). After at least 4 days on this schedule
the subjects were given two days each of 100 retraining trials

according to the O-I procedure, and on the third day, after 50

reinforced trials, extinction responding was recorded for 15 min.

Two days later the animals were tested for spontaneous recovery for

5 min. Two non-contingent priming trials were then given to see

if the animal would resume responding. If responding did not resume,

the animal was re-shaped. Fifty reinforced trials were then given

and subsequent extinction responding was recorded for another 15

mins. During this last extinction session, to test whether the extinc-

tion without responding effect could be replicated with a food reward,

two subjects from both group DEP and group AD LIB (designated as group

DEP-B and group AD LIB-B, respectively) were blocked from responding

during the first two minutes of extinction by a sheet of opaque plastic

inserted between the bar and animal. The remaining subjects (designated

as group DEP-NB and group AD LIB-NB) were allowed to respond throughout

the extinction session. In order to counterbalance for the individual

differences within a group, the food maintenance schedules of group

DEP and group AD LIB were switched and the above procedure was replicated

except that previously blocked subjects were extinguished without

blocking and previously non-blocked animals were given extinction with

blocking. Due to equipment breakdown, data was obtained only for 3

subjects in groups AD LIB-B and AD LIB-NB instead of in 4 subjects as

in groups DEP-B and DEP-NB.

Results and Discussion

Experiment II

Figure 3 and Table 2 show the extinction and spontaneous recovery scores of group DEP and group AD LIB. The deprived groups had significantly ($p<.001$) greater resistance to extinction than the AD LIB group and significantly ($p<.001$) higher spontaneous recovery. This finding supports previously reported increased resistance to extinction under deprivation conditions (Heathers and Arakelian, 1941; Perin, 1942; Saltzman and Koch, 1948).

After the spontaneous recovery session, subjects in groups DEP and AD LIB were given two non-contingent reinforcements. This is analogous to priming trials that are used to elicit responding for ESB. Of the 6 animals that were tested from group O-I, 5 returned to the bar in the first minute after the priming reinforcements. Five of seven AD LIB subjects also returned to the bar in the first minute. It thus seems that the same type of motivation inducing priming effect as is found with ESB can be demonstrated with a conventional reward. The relatively low spontaneous recovery score of group AD LIB (Fig. 3) suggests why priming may sometimes be necessary to induce animals maintained at a low drive level to respond for ESB.

Experiment III

In a presentation of evidence for the drive-decay hypothesis of ESB maintained behavior, Howarth and Deutsch (1962) stated that extinction
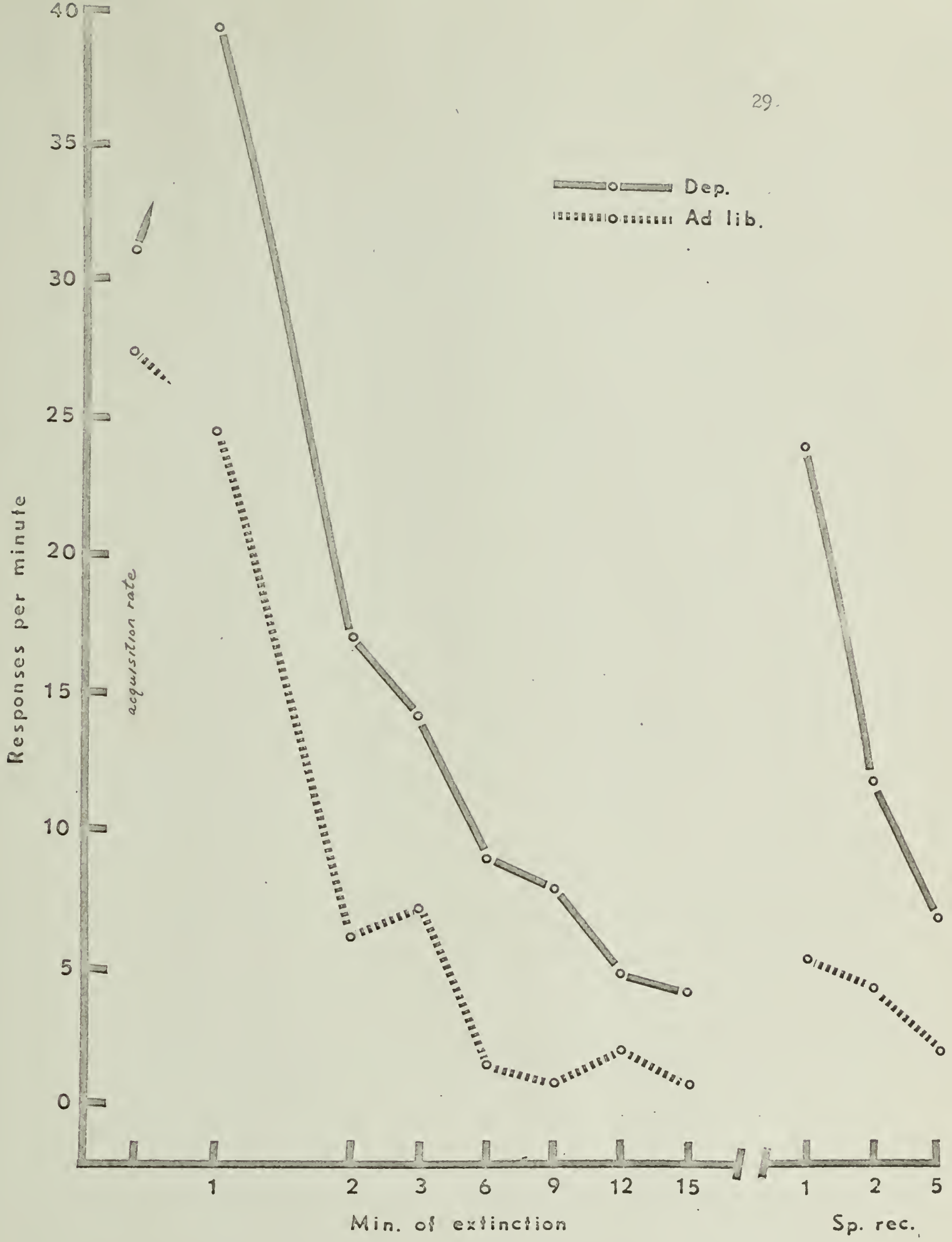
Fig. 3.   Extinction and spontaneous recovery scores for animals
          maintained on 23 hr. deprivation vs. animals on <u>ad lib</u>.
          food.   Responses are represented by 1-minute means on
          the left and 3-minute means on the right.

Table 2. Individual scores and group means for the 15 min. extinction and 5 min. spontaneous recovery periods of Experiment II.

S's	Extinction		Spontaneous Recovery	
	AD LIB	DEP	AD LIB	DEP
1	44	98	14	51
2	35	218	14	51
3	81	182	28	38
4	56	70	35	19
5	87	295	16	110
6	69	90	11	39
7	34	158	2	51
8	46	83	6	59
ΣX	452	1194	126	418
$\bar{X}$	56	149	16	52

should be a simple function of time since the last electrical
stimulus and would be independent of the number of unreinforced lever
presses occuring in that time. Figure 4 and Table 3 present some
evidence that extinction without responding can be induced in an
animal under a low drive state whose responding has been maintained
by the incentive properties of the reward. The extinction responding
of group DEP-B was significantly ($p < .057$) higher than the responding
of group DEP-NB during the last 13 min. of extinction. Extinction
responding for group AD LIB-B, however, did not significantly ($p > .200$)
differ from the last 13 minutes of responding of group AD LIB-NB.
Although this effect should be replicated with naive animals, the
present data suggests that a process similar to the one demonstrated
in ESB animals is also working in animals maintained on a free-feeding
schedule who are working for an intraorally administered high incentive
food reward.

Observations and Conclusion

Incidental observations during and after this experiment revealed
striking similarities between rats rewarded by direct oral injections of
a highly palatable solution and rats rewarded by ESB to certain brain
areas, particularly the lateral hypothalamus and Medial Forebrain
Bundle. The oral subjects displayed an unusually high amount of agita-
tion as reflected by bar biting and rapid changes in position. These
effects increased as the quantity of the injected solution decreased,
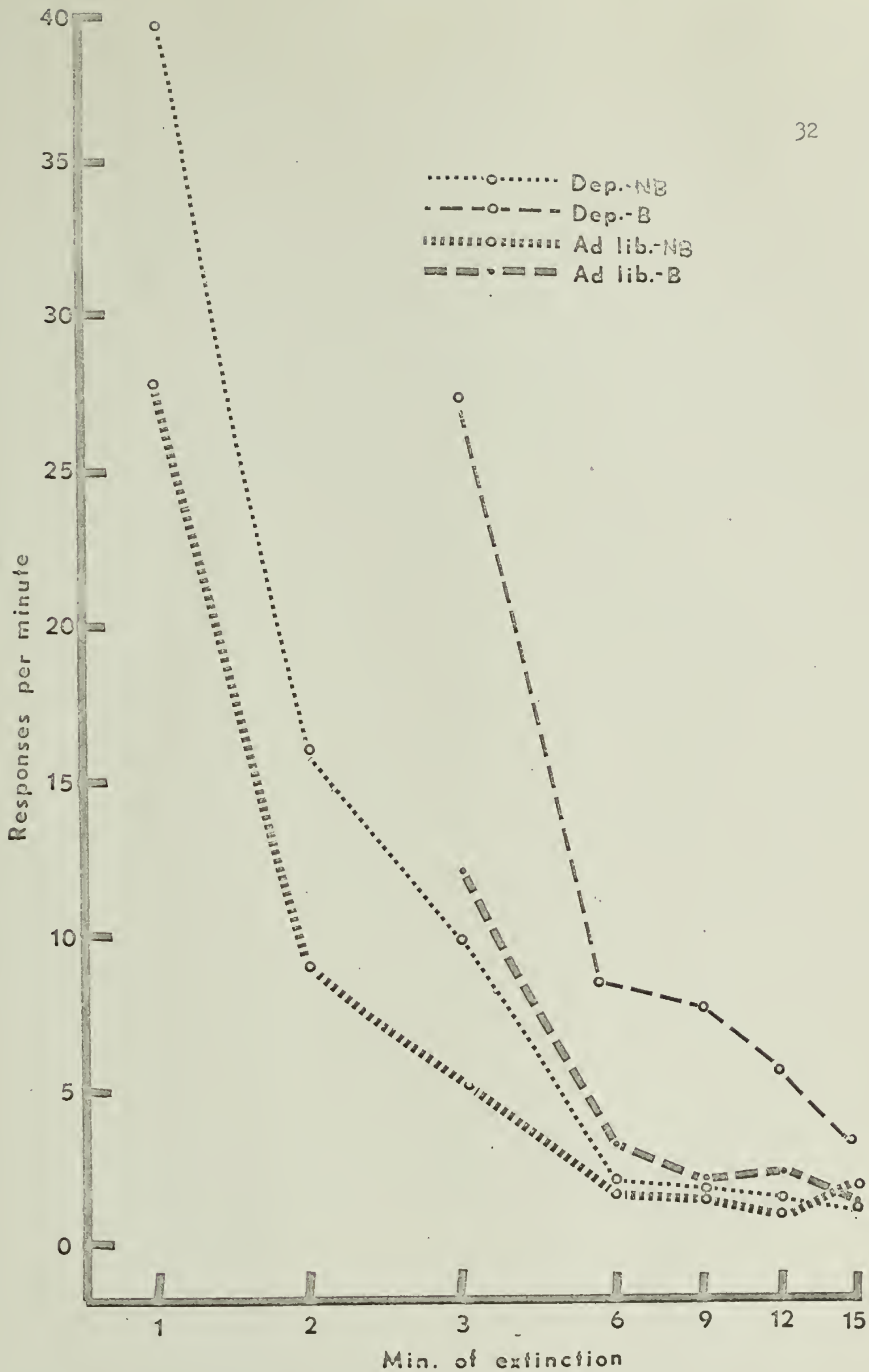
Fig. 4. Extinction scores for animals that were blocked during
the first two minutes of extinction compared to animals
that were allowed continuous extinction

Table 3. Individual scores and group means for number of responses during the 15 min. extinction session of Experiment III. Letters under the extinction conditions designate blocked (B) and non-blocked (NB) conditions. Responses under NB-13 represent the responses during the last 13 min. of extinction for NB subjects.

			Extinction Condition		
Group	S's		B	NB	NB-13
	1		26		
	2			118	33
	3		144		
	4			89	20
DEP	5		179		
	6			82	35
	7		58		
	8			77	17
		X	407	366	105
		X̄	102	92	26
	1			**	**
	2		**		
	3			86	26
	4		45		
AD LIB	5			60	35
	6		36		
	7			27	4
	8		25		
		X	106	173	65
		X̄	35	57	22

** Data not collected because of equipment breakdown

but decreased across sessions. Another striking aspect of the behavior was that if the animals were put on a 10 sec. fixed interval schedule, responding was maintained during the reinforcement-off periods, and it became more agitated and was completely indistinguishable from the most agitated behavior maintained by ESB.

After the experiments, observations were also made of water deprived animals responding for intraoral water injections. Animals working for water could be differentiated from those working for chocolate milk. While working for food animals would both lick and bite the bar, but while working for water animals almost invariably licked the bar. This observation may have implications for understanding the nature of the stimulation in animals working for ESB, since they also have characteristic modes of responding such as biting the bar or licking it.

Direct comparisons between food deprived animals and animals responding for ESB are difficult to make because of our present inability to specify the amount of self-stimulation that is equivalent to a certain quantity of food reward (Pliskoff, et al., 1965). It seems, however, that by the manipulation of drive level and qualitative and quantitative incentive variables, much of the behavior elicited from animals rewarded with ESB can be approximated with the intraoral self-injection preparation and conventional rewards. The behavioral similarities that have been so far demonstrated are rapid acquisition, rapid extinction, agitation and excitement accompanying responding,

priming effects, and extinction without responding. Since the rapid

extinction and extinction without responding were only demonstrated

in animals maintained at a low drive level, it seems that the satiated

animal whose behavior is maintained by the immediacy and incentive

quality of the reward is most similar to animals whose behavior is

maintained by ESB.

General Discussion and Conclusions

Since the data that most closely resembled data collected in ESB situations was obtained from freely fed animals (groups AD LIB and AD LIB-B), whose behavior was maintained by a highly palatable reward, there is a possibility that there is a strong incentive or expectancy component elicited in the two preparations which is the crucial similarity between them. The variables of delay, amount and palatability of reward have long been recognized as contributors to incentive motivation (Spence, 1956). Since the quick extinction of ESB maintained behavior is the most striking of its "unique" properties, it is of interest to know how the various incentive variables affect extinction responding for conventional rewards.

Early studies (Zeaman, 1949; Lawrence and Miller, 1947; Metzger, 1957) reported that amount of reward during acquisition had no affect on subsequent extinction. More recent studies (Armus, 1959; Ison and Cook, 1964), however, have found that the larger the magnitude of reinforcement in acquisition, the less the resistance to extinction. Hulse (1958) demonstrated that a large reward produced greater resistance to extinction than a samll reward if partial reinforcement was used in acquisition, but less resistance to extinction if continuous reinforcement was used. Wagner (1961) and Laretsky (1965) confirmed these findings.

Increasing delay of reinforcement in runway situations has clearly been directly related to increased resistance to extinction (Crum et al., 1951; Fehrer, 1956; Peterson, 1956; Sgro and Weinstock, 1963).

Quality of reward has not been as extensively studied as the other two variables, and it may be the most important. Although running speed and bar-pressing rate have been shown to increase with increases in the quality of reward (Hutt, 1954; Goodrich, 1960; Knarr and Collier, 1962), extinction has hardly been investigated. Two studies were found that reported greater resistance to extinction with a reward of higher quality during acquisition (Guttman, 1953; House, 1964). This is an opposite effect as compared to results found with studies that increased the incentive by increasing quantity of reward or by decreasing delay of reward. It should be noted, however, that these studies used deprived animals. No study has reported data where extinction measures were taken on satiated animals. Comparisons in such groups may produce entirely opposite results.

In looking at the extinction data from these studies that varied incentive motivation, it seems that the most inclusive explanation for the data is derived from frustration theory. Unfortunately there is little general agreement about what the antecedents and consequents of frustration are in specific situations; nor is there agreement on a unitary mechanism of frustration.

Implicit in the concept of incentive-frustration is the postulate that the greater the incentive during acquisition, the greater the frustration engendered by its removal. It has been demonstrated that the greater the strength of frustration, the faster the extinction of a non-rewarded response. Thus, frustration

is viewed as an energizer of extraneous behavior, and hence leads

to a decrease in instrumental responding. Only in situations where,

during acquisition, an animal has been induced to maintain responding

in the face of cues of frustration, will frustration sustain behavior.

Kimble (1961) describes how the theory of frustrative nonreward

explains how intermittent schedules and increasing delay of reward

lead to greater resistance to extinction:

> The effect of frustration is to increase motivation.
> Early in training, before. . . (a) response is firmly
> established, the effect of this motivational increase
> is mainly to strengthen irrelevant and interfering
> responses produced by frustration. This accounts for
> the lowered performance under intermittent schedules
> early in training. With increased practice, however,
> the interfering responses tend to disappear because they
> are never reinforced, and the animal's behavior is
> limited fairly strictly to. . . (a) response which is
> the one most consistently reinforced. When this happens,
> the motivation produced by fustration has only the
> correct response to act on, with the result that partial
> reinforcement now improves performance. In extinction,
> animals previously trained with continuous reinforcement
> are frustrated for the first time, producing interfering
> responses long since abandoned by partially reinforced
> subjects. As a result, the. . . response of the former
> group extinguishes quickly.

A theory for reinforcing brain stimulation has been proposed by

Deutsch (1960, 1963). He proposed that ESB rewards a response and

at the same time produces a drive for more stimulation. Although

the nature of ESB reinforcement can not be evaluated presently

beyond the law of effect, it is compelling that extinction under ESB

reward approaches the type of extinction found when certain incentive

qualities of conventional rewards are maximized. It would thus be

a more parsimonious starting assumption to view ESB as merely a very
high incentive reward. Furthermore, manipulations that have been shown
to prolong extinction in conventional instrumental situations have
recently been replicated with ESB. In the free operant bar-pressing
situation, the delay of reward is usually minimal, and extinction is
rapid. In runways (Olds, 1956), however, and in free operant situations
where ESB is administered after the second link of a chained response
(Pliskoff, et al., 1965; McIntire and Wright, 1965; and personal observa-
tions), extinction responding is strikingly prolonged. This and
Pliskoff's (1965) demonstration of conventional schedules of
reinforcement with ESB seen to be especially devastating to Deutsch's
theory. Drive decay should remain invariant; despite these manipulations.

One strong support for the possibility that there is drive
induction due to rewarding ESB remains. It has been shown that
hypothalamic sites where stimulation produces eating (Margules and
Olds, 1962) and copulation (Caggiula and Hoebel, 1966) also support
self-stimulation. The conclusion that drive is induced here is, however,
not absolutely necessitated. An animal experiencing centrally induced
incentive aspects of a reward may "want" to interact with appropriate
consumatory objects which have been previously associated with similar
feelings. To complicate the issue further, Mogenson (1967) has presented
evidence that suggests that the centrally elicited induction of a drive
may have incentive components of its own in the presence of an appropriate
consumatory object.

It is at present impossible to differentiate rewarding ESB on
the dimensions of quality and quantity of reward. Valenstein (1964)
has demonstrated that the preferrence for stimulation at certain
sites is not correlated to the rate of responding for stimulation
to those sites. Although increasing quantity of food reward has
definitely been shown to decrease extinction responding, increasing
quality has shown the opposite effect. This is a problem for an
incentive-frustration explanation of rapid ESB extinction. It
may be crucial however that this effect of increased quality of
reward has been found with deprived animals. There may be a unique
interaction of this incentive variable with drive variables. To
maintain a consistent incentive-frustration theory, the following
ad hoc hypothesis is made: In satiated animals, whose behavior is
maintained by the incentive quality of the reward, resistance to
extinction will be inversely related to the quality of reward during
aquisition. This hypothesis would pertain only to the CRF situation.
If it holds true to experimental tests, a forceful presentation of
an incentive-frustration theory to explain ESB maintained behavior
could be presented.

Other interesting predictions could be derived from the
incentive-frustration hypothesis. An animal in a CRF self-stimulation
situation essentially never encounters frustration until an extinction
session. It is thus hypothesized that when extinction is initiated,
responding quickly terminates because of extreme frustration.

Adelman and Maatsch (1956) demonstrated that an animal will
prolong extinction responding in a runway if it is allowed to
extricate itself from the frustration of an empty goal box by
jumping out. Possibly the size of a self-stimulation chamber
might be a crucial variable in extinction responding. The smaller
the chamber, the more an animal is confined in a frustrating
situation. With a large chamber, extinction should be prolonged.

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Appendix A

The Fluid Injection System

I. The electro-fistular swivel

The swivel (Fig. 5-A) is a modification of the one described
by Johnson, Trehub and Pietskowski (1966). By making the electrode
contacts onto two ball-bearings that are insulated from each other
(P, F & G), but which rotate together on a hollow core bolt (O & S)
containing the injection tubing (N), the independence of the fluid
injection system is maintained while twisting of the electrode lead
is prevented. The hollow core bolt system is completely constructed
from common electrical hardware such as tip jacks and banana jacks.

The swivel is most easily assembled in two sections. 1) The
hollow core swivel system: The tube springs (R) are soldered to the
outside rims of the ball-bearings (C). This connection may be made
either with one of the liquid metals such as Epoxy Liquid Steel or
with acid-core solder. The heat necessary in making an acid-core
solder connection is not sufficient to damage the ball-bearings. The
protective vinyl spaghetti tuing (H) is friction fitted into the non-
insulated banana jack (O) and the hollow bolt of the insulated banana
jack (S). The following pieces are then slipped onto the non-insulated
banana jack (O): a solder lug, the insulating washer from the insulated
tip jack (G) and another solder lug. The second solder lug must be
reamed out to fit over the protruding lip of the insulating washer. In
this way it will be insulated from the metal parts of the hollow core
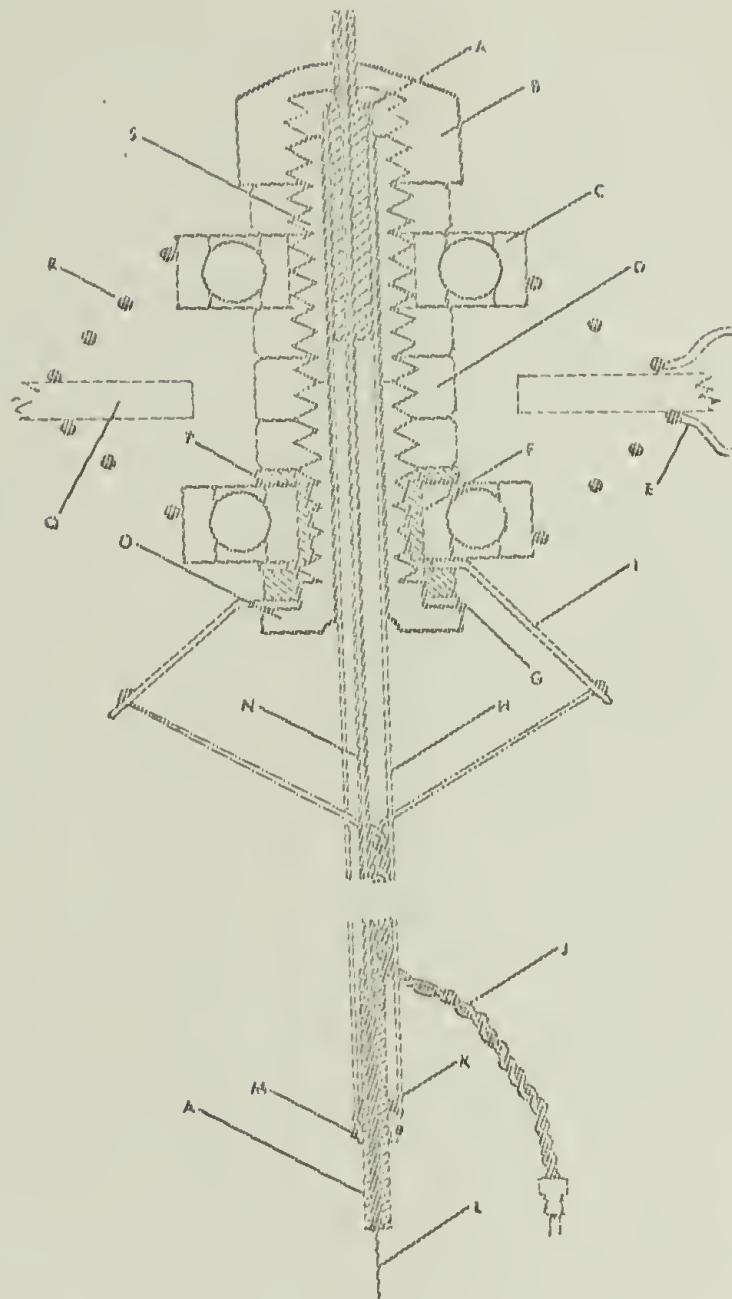bolt that conduct the electricity from the top ball-bearing to the

Fig. 5. Cross section view of the electro-fistular swivel.
A) concentric layers of Thermofit tubing, B) plastic
cap from insulated tip jack, C) ball-bearing, D) nuts
from banana or tip jacks, E) Lead from stimulator,
F) Thermofit or electrical tape insulating sleeve,
G) plastic insulating washer from insulated tip jack,
H) 3/16 in. outside diameter protective vinyl spaghetti
tubing, I) solder lug, J) electrode lead, K) spacer,
L) stainless steel needle tubing, M) wire binding,
N) polyethylene tubing, O) non-insulated banana jack,
P) insulating washer, Q) plexiglass swivel mount,
R) spring from vacuum tube protective cover, S) threaded
bolt from insulated banana jack.

bottom solder lug. A few threads of the non-insulated banana jack (O) are filed away, and electrical tape (F) is wrapped around the area. Thus when the bottom ball-bearing is positioned as shown (Fig. 5-A), it too will be insulated from the non- insulated banana jack (O). Complete insulation is accomplished by a cardboard washer (P) placed on top of the journal of the bottom ball-bearing. The journal is then firmly attached to the banana jack (O) by nuts (D). The two parts of the hollow core bolt (O & S) are now joined by a nut. This part of the swivel is inserted through a hole in the plexiglass swivel mount (Q) as shown in Fig. 1-B, and the top ball-bearing, with its attached springs, is positioned on the bolt from the insulated banana jack (S). The springs (R) thus suspend the swivel on the plexiglass (Q). Fig. 5-B, an exploded perspective drawing of the swivel, should help visualize the spatial relations of the swivel, especially the connection of the springs to the ball-bearings. The friction of the springs on the plexiglass is much greater than the friction of the ball-bearings. Hence the hollow core bolt turns with the protective vinyl tubing that is friction fitted into it. 2) The inner fluid transport and electrical stimulating system: Concentric layers of Thermofit (A), a heat shrinkable tubing, are shrunk around the polyethylene tubing (N) at its distal ends so that the fluid transport system will be reinforced and will fit snugly into the protective tubing (H). After the fluid transport system has been inserted into the protective vinyl tubing, electrode leads are threaded into the protective tubing through appropriately placed holes. The fistulated

Fig. 6. Exploded perspective view of the swivel. Labeling corresponds
to that used for Fig. 5. A) concentric layers of Thermofit
tubing, B) plastic cap from insulated tip jack, C) ball-bearing,
D) nuts from banana or tip jacks, I) solder lug, O) non-
insulated banana jack, P) insulating washer, Q) plexiglass
swivel mount, R) spring from vacuum tube protective cover,
S) threaded bolt from insulated banana jack.

animal is connected to the fluid transport system by a short length of hypodermic needle tubing (L). Since the protective vinyl tubing is bound (M) to the reinforced ends of the polyethylene tubing, the turning of the animal is translated into the rotation of the swivel and the delicate polyethylene tubing is protected from being torn or crimped.

In its assembled form, fluid input to the fluid transport system is accomplished by a short length of hypodermic needle tubing (F-fig. 8). The swivel rotates easily around the needle tubing with no leakage. The springs attached to the ball-bearings allow overall resiliency of motion to the swivel as it follows the movements of the animal. The swivel can be dismoundted easily for servicing by unscrewing the plastic cap (B) and the first nut. Since the tube springs (R) are not attached to the plexiglass mount, the top ball-bearing may be lifted off the banana jack bolt (S).

The dimensions of the components used in this swivel are as follows: potective vinyl tubing--3/16 in. outside diameter, 2/16 in. inside diameter; polyethylene tubing--PE-50; hypodermic needle tubing-- 23 gauge. Banana jacks and tip jacks fitting a 3/16 in. mounting hole were used. The following components were used for the various jacks. Allied Electronics (Chicago, Ill.) stock numbers and Fig. 4 labels are included for all components used: O--Non-insulated banana jack (A (185); A--threaded bolt from insulated banana jack (24 A 9169); B--insulated plastic cap, and G--plastic insulating washer from insulated tip jack (24 A 9163).

II. Methods of coupling the animal to the injection system.

Two reliable methods of coupling the animals to the injection system were developed (Fig. 7). If the bare polyethylene fistula is brought through the acrylic cement cap on the animal's head, it will break off with minimal flexing. A durable female unit can be formed, however, by molding several concentric layers of Thermofit tubing (B) around the polyethylene fistula (Fig. 7-A). The Thermofit may be coated with Epoxy cement before shrinking to form a more durable unit. A length of needle tubing has to be inserted into the polyethylene tubing (C) while shrinking the Thermofit to prevent the fistula from collapsing. The tubing should be shrunk with a low wattage soldering-iron or cautery to prevent splitting. The end of the fluid transport tubing from the swivel is formed into a male unit which can be attached to the female unit on the animal's cap. The connection is bound by shrinking a sleeve of Thermofit around the protruding collars as shown in Fig. 7-A. The animal can easily be disconnected from the injection apparatus by cutting at the joint with wire strippers. This coupling system was used in the previous experiments.

The second type of connecting system we have used is a direct generalization of the system used with a type of commercial electrodes (Fig. 7-B). The plastic couplers (D) that are used with these electrodes have been bored out to accommodate the polyethylene fistula. A commercially produced threaded collar (E) is used to connect the couplers.
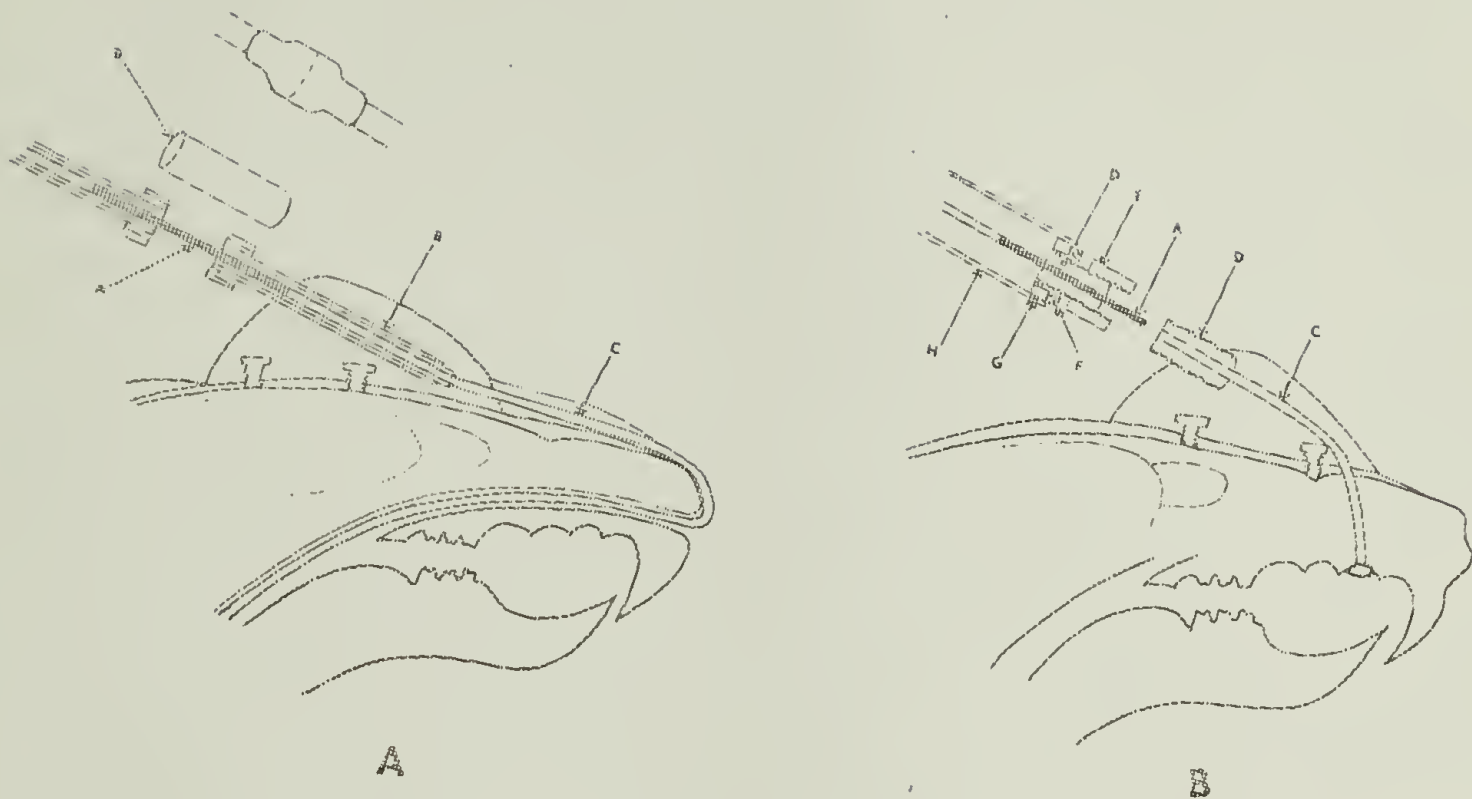
Fig. 7. Two methods of coupling fistulated animals to the fluid
injection system: A) stainless steel needle tubing,
B) Thermofit tubing, C) polyethylene tubing, D) plastic
coupler, E) coupler connector collar, F) wire binding,
G) spacer, H) protective vinyl spaghetti tubing.

III. Injection apparatus.

In these experiments the electro-fistular swivel was mounted on the cover of a standard rat chamber. Figure 8 shows the swivel in functional relation to the injection apparatus. A solenoid-driven syringe is connected to the input of the swivel through a two way Aupette valve (D). Fluid is drawn from a reservoir (C) during the spring return of the solenoid arm. The injection syringe is held firmly between a bracket(G) and a clamp (B). Care was taken in choosing the spring for the solenoid arm return, so it was strong enough to return the solenoid arm but weaker than the maximum lift of the solenoid. In this experiment a 24 VDC continuous duty Guardian solenoid with a 66 oz lift was used. A layer of oil (A) was floated in the syring barrel to prevent freezing of the syringe.
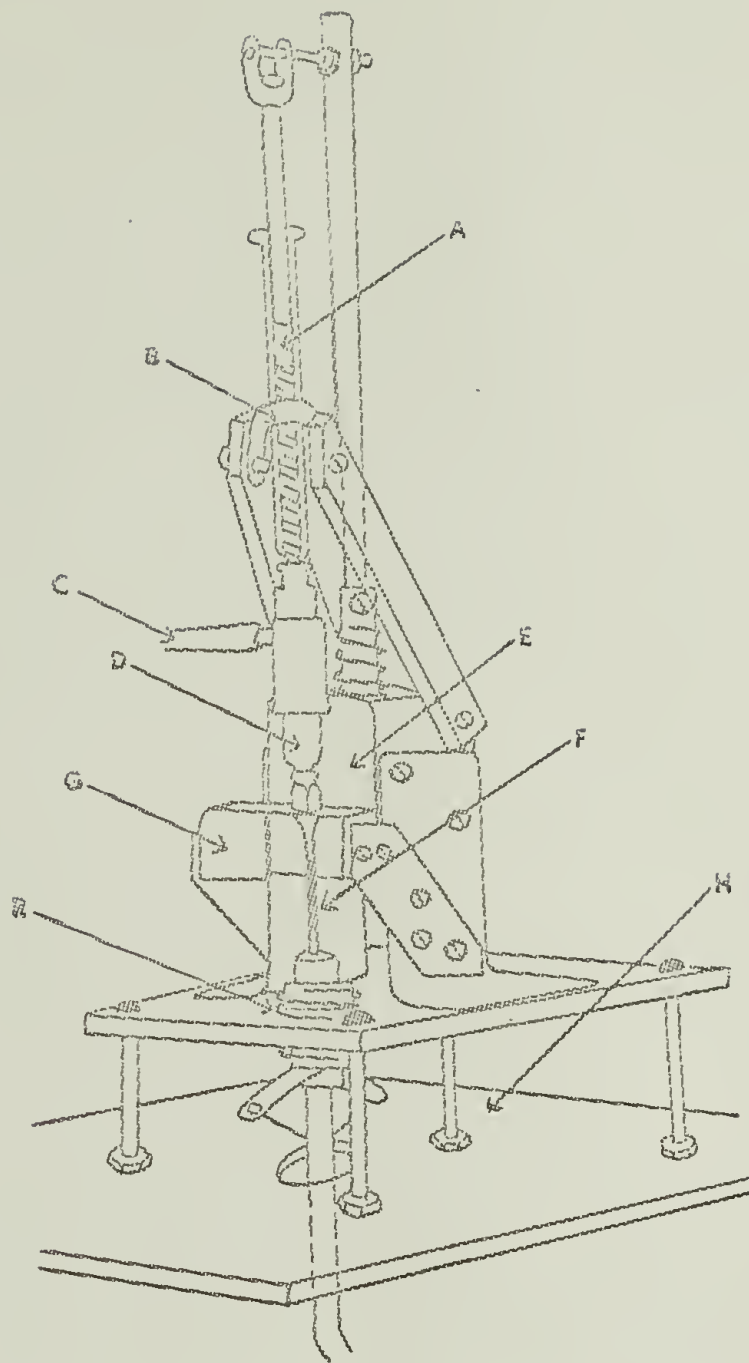
Fig. 3. Electro-fistular swivel with the injection apparatus; A) a layer of light vegetable oil to prevent freezing of the syringe piston, B) clamp, C) to fluid reservoir, D) Aupette valve, E) solenoid, F) hypodermic needle tubing, G) metal bracket, H) cover of training chamber, R) vacuum tube spring attached to a ball-bearing of the swivel.

Appendix B

Operative Procedures

I. Intragastric fistula

Implantation of the gastric fistula was based upon the method described by Epstein and Teitelbaum (1962). Animals were anesthetized with pentobarbital (40 mg/kg, IP) and injected with .2 cc Atropine Sulfate to prevent excessive secretion by the mucous membranes. The posterior portion of the skull was exposed by a midline incision and three jewlers screws were screwed to the cranium. A preassembled gastric tube was next threaded down the nasopharynx and esophagus to a point near the cardiac sphincter. The other end of the tube was threaded under the skin of the snout and brought out at the incision on top of the skull. The gastric tube itself consists of two lengths of polyethylene tubing (PE-50) which are approximately 5 in. and $2\frac{1}{2}$ in. long. Both lengths of tubing are friction fitted onto U shaped elbow of stainless steel needle tubing (23 gauge), and the joint is connected by shrinking a sleeve of Thermofit tubing over it. The external end of the fistula is reinforced with concentric layers of Thermofit tubing (Fig. 8-A) after the fistula has been placed in position in the animal. Finally the assembly was secured in position by a mound of acrylic cement surrounding it and the stainless steel screws.

II. Oral fistula

This pocedure is based on the method described by DeBold, Miller and Jensen (1965). A fistula is prepared by friction fitting a seven

inch length of stainless steel tubing (external diameter .034 in.) into a five inch length of PE-100 polyethylene tubing. The free end of the polyethylene tubing is then momentarily held over a flame to flange the end slightly. The stainless steel tubing is later used to guide the fistula through the nasal bones.

It has been found that the operation is best performed on large animals whose nasal bones are well developed. Animals were anesthetized with pentobarbital (40 mg/kg, IP) and injected with .2 cc of Atropine Sulfate to dry mucous membranes and facilitate breathing. The top of the head and snout were shaved, and the animal was mounted in a stereotaxic to assure ease and stability in drilling. A long medial incision was made on the snout and continued almost to bregma. The nasal bones and skull were exposed. A guage No. 6 hole was drilled in the nasal bone about midway between a line connecting the eyes and the naris, so positioned as not to rupture either the midline bone suture or the adjacent lateral suture. The hole was drilled slowly, care being taken to avoid sudden penetration or the rupture of either suture. It was found helpful to use an electric dental drill for this hole. Drilling was delicately continued until, by feeling with a needle probe, it was certain that no bone was still attached to the perimeter of the hole. Heavy bleeding usually occurred at this point but it was usually restricted to the skull and blood did not enter the oropharyngeal cavities. Three additional holes, well spaced in a triangle, were drilled into the skull and nasal bones, and stainless steel screws were screwed into these holes. The animal was then removed from

the stereotaxic and its throat was cleaned of any accumulated mucus with a suction bulb.

Next the stainless steel needle tubing with the attached poly-ethylene fistula was threaded into the rat's mouth. The animal's mouth was held open and the sharpened end of the needle tubing was placed against the palate between the second and third palatal ridges at a point slightly lateral to the animal's midline and directly below the hole in the nasal bone. The needle tubing was forced upward through the roof of the mouth and guided through the hole in the nasal bone. Care was taken to damage as little tissue as possible. The needle tubing is drawn up through the snout until the flange of the attached polyethylene fisula fit snuggly between the ridges of the upper palate.

There appears to be a sinus at the midline which when ruptured results in profuse bleeding, often from both nostrils. Failure to thread the hole on the fist try did not usually result in failure. It was possible to move the tip of needle tubing carefully to locate the hole. If the bleeding was very strong, the needle tubing was removed and the animal's nasopharynx throughtly suctioned clear of blood before continuing. Though the bleeding was usually severe, pulmonary congestion was prevented by holding the animal with its head down while suctioning out the throat and nostrils. After the animal stopped bleeding, threading of the fistula was resumed, if it had not been successful on the first try.

When the fistula had been successfully threaded, the screws and nasal bone were thoroughly dried and cauterized. Concentric rings of Thermofit

tubing were shrunk around the external end of the fistula (Fig. 8-A) to give a firm outlet that could readily be coupled to a liquid dispensing apparatus. The stainless steel tubing was now removed and the polyethylene fistula was held at 30° angle to the skull. A mound of acrylic cement was built around the fistula and the anchoring screws.

After the operation a .2 cc, intramuscular injection of Bicillin was given each animal to prevent infection.