1-1-1971

Electrically elicited behavior in the rat : sources of reinforcement.

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ABSTRACT

The eating, drinking and gnawing behavior induced by electrical stimulation of the lateral hypothalamus (ESLH) in rats was studied in order to assess the role of reinforcement in controlling the behavior. In the first study, an attempt was made to modify the initial stimulus-bound behavior to emerge by giving the animal previous experience with the drinking response in the presence of ESLH. The results showed that a contiguous relationship between a 30-second train of ESLH and the performance of a drinking response was not sufficient to modify the type of stimulus-bound behavior to initially emerge.

A second set of experiments examined the role of ESLH as a reinforcer in stimulus-bound behavior by allowing animals in a shuttle apparatus to choose between various stimulation conditions and no stimulation. The results indicated that most animals had a slight preference for long durations of ESLH.

In the final experiment stimulus-bound animals were trained to bar press for 3 second trains of ESLH that would elicit the stimulus-bound response. The bar press rate was then measured with the appropriate goal object

present where the animal could perform the consummatory response and in a situation without the goal object present where the animal could not make the response. Stimulus-bound gnawers, as well as eaters and drinkers, all bar pressed more when they could perform the consummatory response, hence supporting the notion that the performance of the response is reinforcing in electrically induced behavior.

This research supported an interpretation which suggests that the behaviors elicited by ESLH are maintained by reinforcement arising from the incentive qualities of the goal object, the ESLH itself, and the performance of the response. It was suggested that future research should explore the ESLH as a reinforcer in stimulus-bound animals under conditions that maximize the strength of the reinforcement (ie. where the animals regulate the rate and duration of the stimulation).

ELECTRICALLY ELICITED BEHAVIOR IN THE RAT: SOURCES OF REINFORCEMENT

A Dissertation Presented

by

Drake C. Chisholm

Submitted

to the

Graduate School

of the

University of Massachusetts

in partial fulfillment

of the

requirements for the degree

of

DOCTOR OF PHILOSOPHY

July 1971

Major Subject Psychology

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July, 1971

ACKNOWLEDGEMENTS

I would like to thank Dr. Jay Trowill, my dissertation advisor, and the members of my dissertation committee, Dr. J. Moore and Dr. N. Carlson, for their time and advice. I would especially like to thank Dr. Jay Trowill for his numerous insights and guidance.

D. C. C.

July 1971

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GENERAL INTRODUCTION

A Motivational Interpretation of Electrically Elicited Behavior

Psychologists interested in the motivational aspects of behavior have found electrical stimulation of the brain, especially in the region of the lateral hypothalamus (ESLH), to be a most useful research technique. In a number of species ESLH produces a well-organized behavioral pattern. One of the earliest demonstrations of this phenomenon was reported in 1943 by Brugger who found that ESLH elicited eating in the cat. In most cases the animals ate both edible and inedible materials during the period of stimulation and for as long as 20 minutes after the offset of the stimulation.

Typically, normal feeding behavior has been used as evidence for the presence of a hunger drive. Therefore with the emergence of feeding induced by ESLH most psychologists tended to apply the same hunger drive explanation that had been applied to eating normally elicited by food deprivation (Miller, 1957,1960).

Some of the most convincing evidence for the drive-like qualities of brain stimulation came from a study where the electrodes were placed just lateral to a line between the fornix and the mammalothalamic tract at the

rostrocaudal level of the ventromedial nucleus (Miller, 1961). It was found that food satiated but mildly thirsty rats would leave a drinking tube and perform a previously learned food-seeking response during stimulation of these points. Thus the eating elicited by ESLH was similar to a specific drive to eat food and it did not appear to be an indiscriminate chewing response as Smith (1956) had proposed earlier.

Other results have shown that ESLH-induced eating is under the control of taste stimulation in a fashion similar to that of deprivation-induced eating. Coons (1963) has reported that rats show preferences for particular solutions when stimulated. For example, an individual rat that drinks a solution containing sugar will not drink water or a solution with salt. Recently, Phillips and Mogenson (1968) have found that saccharin increases intake while quinine decreases intake during ESLH.

Additional research indicates that the same ESLH that elicits hunger can elicit a learned food seeking response. For example, when food deprived animals trained to bar press for food on a variable interval (VI) schedule are subsequently satiated and then stimulated in the lateral hypothalamus they will respond appropriately on the previously learned VI schedule (Miller, 1960). Furthermore it has

been demonstrated that the learning of a new maze response for food can be motivated by the same ESLH that elicits "hunger" (Mendelson and Chorover, 1965).

Other research by Miller (1961) showed that ESLH in food satiated rats caused them to eat approximately twice their daily ration. As the volume of food consumed increased, the threshold for inducing additional eating also increased. Therefore it appears that eating produced by ESLH was affected by both the faciliatory feedback from the mouth and the inhibitory feedback from the stomach in a manner similar to the normal feeding response.

Other evidence has indicated that appetitive responses elicited by ESLH vary with stimulation in a way that would be expected if there were a correspondence between current intensity and the degree of food deprivation. Coons (1963) found that over a range of ESLH intensities there was a corresponding change in the rate of food pellet consumption. Also, Tenen and Miller (1964) showed that increasing either hours of deprivation or intensity of ESLH produces an increase in an animal's tolerance for quinine mixed in milk.

Miller (1960) also reported that D-amphetamine which reduces normal hunger also increased the current threshold required to elicit ESLH-induced eating in satiated rats.

This was interpreted as support for the equivalence between deprivation-induced hunger and ESLH-induced "hunger".

Schlosberg and Pratt (1956) showed that some stimuli act as secondary reinforcers only when animals are hungry. Fantl and Schuckman (1967) replicated the earlier finding, however ESLH was substituted for hunger and analogous effects were obtained, suggesting a strong resemblance between ESLH and hunger.

Finally, Coons, Levak and Miller (1965) reported that satiated animals given ESLH learned a discriminated bar press response for food and that they also pressed the correct bar when under 48 hours of food deprivation. Thus, there is considerable evidence for the notion that ESLH can motivate instrumental behavior and that there is transfer between ESLH-produced hunger and normal hunger.

Evidence Against a Specific Motivational Interpretation

Over the last fifteen years numerous studies have indicated that electrical stimulation of the hypothalamus is capable of inducing a variety of behaviors in satiated animals. Some of the specific behaviors elicited have included eating (Coons, 1963), drinking (Greer, 1955), attack (Panksepp and Trowill, 1969), gnawing (Roberts and Carey, 1965), and copulation (Vaughan and Fisher, 1962).

Usually the elicited behavior begins a few seconds after the onset of stimulation and terminates with the offset. Due to the fact that the behavior is under the strict control of the stimulation, Valenstein, Cox and Kakolewski (1969) have applied the term "stimulus-bound" behavior. In keeping with Miller's drive notion, many investigators have assumed that the elicited behaviors were a result of the stimulation of neural pathways associated with specific states such as hunger, thirst and sexual arousal. However, more recently, Valenstein et al. (1970) have reported that ESLH may produce many "unscoreable" behaviors including tail preening, food shuffling and hoarding. Explanations such as that of Miller's, that rely on intervening motivational variables, are now obliged to hypothesize the existence of tail preening and food shuffling drives. This recent increase in the number of specific motivational states that may be elicited from the same anatomical site decreases the likelihood that the underlying substrate is divided into independent systems at the level of the hypothalamus.

Furthermore, in 1968 Valenstein et al. reported a most important experiment involving stimulus-bound eating, drinking and gnawing. In contrast to Miller's (1957,1960) procedure Valenstein equipped his test chamber with three goal objects: large food pellets (Purina Lab Chow), a bot-

tle containing water with a metal drinking tube, and a wooden wedge. Thus Valenstein reported the emergence of three primary behaviors: eating, drinking and gnawing. Then by simply removing the initial goal object from the test chamber Valenstein found that it was always possible to shift the initially evoked behavior to one of the other goal objects. Due to the fact that the stimulus parameters had not been changed and that the second behavior was as reliable as the first, it was concluded that the activation of the same underlying "neural circuits" could elicit a variety of behaviors. Thus, according to these results, it was illogical to think of a stimulus as specifically eliciting either hunger, thirst or gnawing when the consummatory response could be shifted from drinking to eating or gnawing.

An Alternative Hypothesis to the Motivational Interpretation

Prepotency. The normal drive theories (Miller, 1957, 1960) have never resolved the conflict as to why an animal should press a bar to evoke hunger. This paradox coupled with the finding that stimulus-bound eaters can be switched to stimulus-bound drinkers when the food is removed led Valenstein (1969,1970) to conclude that the postulation of specific motivational states related to biological

needs may not be justified. Instead, Valenstein prefers to view behavior elicited by hypothalamic stimulation as "prepotent responses". These prepotent responses are assumed to be relatively high in an animal's "response hierarchy" and are the most likely responses to be elicited by ESLH. Thus, Valenstein's new term, prepotency, is circularly defined.

Although the precise features of the situation that may contribute to response prepotency were not fully discussed it was suggested that both the activation of a neural substrate and certain environmental factors may affect the degree to which a particular response is prepotent. However, previous research suggests that one cannot predict the type of behavior that will be evoked on the basis of electrode placement within the lateral hypothalamic area (Valenstein, Cox and Kakolewski, 1970). Thus the only remaining test of the prepotency hypothesis at this time is apparently via various environmental manipulations.

It may be that the procedure Valenstein used to screen his animals has biased the type of behavior that emerged by allowing environmental factors to influence the prepotent responses. First, the animal was stimulated for an unspecified period of time during which intensity par-

ameters were adjusted and responses to the stimulation were observed. If no specific behavior pattern emerged the animal was placed on what was called a night schedule. This consists of a 12 hour period during which the animal was stimulated for 30 seconds every 5 minutes. If no stimulus-bound behavior emerged the animal was placed on the night schedule again during the following night. All animals received a minimum of two night schedules before an electrode was classified as ineffective. Owing to the fact that rats are nocturnal animals and that they do not remain satiated throughout the entire night session (12 hr.) it was likely that eating and drinking, as opposed to other behaviors, were more highly correlated with the stimulation during this schedule.

This procedure was in marked contrast to that used by Flynn (1967) with cats and Panksepp and Trowill (1969) with rats displaying attack behavior. The attack response was apparently evoked on the first few test trials and prolonged screening procedures were not necessary. Similarly, in our laboratory some rats displayed stimulus-bound eating or gnawing at the outset of testing; however, many animals required a prolonged "screening" period before any stimulus-bound behavior emerged. For the animals that required a long stimulation period it seems likely that certain experiences during training may have influenced

the final form of behavior that emerged.

Valenstein and Cox (1970) have attempted to manipulate prepotency by manipulating the animal's deprivation state and to observe its effects upon the behavior that was evoked during the initial stimulation experience. Animals were deprived of either food or water and then tested to determine if the deprivation state would influence the form of stimulus-bound behavior that emerged. The results showed that food deprived animals that were consuming food during and between stimulation periods were equally likely to become stimulus-bound drinkers as they were to become stimulus-bound eaters. It was concluded that stimulation presented together with the act of eating or drinking was not a sufficient condition for the establishment of a particular stimulus-bound behavior, ie., prepotency was apparently not affected by these manipulations.

The Role of Reinforcement in Maintaining Electrically Elicited Behavior

Until recently, Valenstein has been predominantly concerned with ways of influencing the type of stimulus-bound behavior that initially occurs. Thus the question of the maintenance of stimulus-bound behavior has been left unanswered. Considerable evidence is available

suggesting that on-going stimulus-bound behavior is affected by reinforcement. For example, many animals require a long period of screening during which they appear to "learn" to emit the most rewarding behavior. Also, Valenstein et al. (1969) found that if both electrodes are effective in bilaterally implanted rats, then the same behavior is usually elicited from both electrodes. This finding is consistent with the notion that the response which occurred when the first electrode was active was strengthened with repeated stimulations and that the second electrode elicited the same response due to generalization.

One line of evidence that suggests that reinforcement is present in stimulus-bound behavior comes from studies where the initial stimulus-bound response was switched to a new behavior. Smith (1969) and Valenstein (1970) showed that rats which received extended experience with the initial goal object did not switch to a new response as quickly as animals which did not receive the extended experience. The extended experience with the initial goal object appeared to strengthen the first response. Then when the original goal object was removed an extremely strong initial response tendency had to be overcome before a new response would emerge. Therefore

the second purpose of this research was to examine such factors as reinforcement which may play a role in strengthening stimulus-bound behavior once it has emerged.

Valenstein et al. (1970) have recognized the role of reinforcement in maintaining and modifying stimulus-bound behavior; however, they have recently chosen to emphasize the importance of the response as a source of reinforcement in stimulus-bound behavior. Extensive pilot data in our laboratory suggested that both the nature of the goal object and the electrical stimulation itself also play an important role in maintaining stimulus-bound behavior.

The goal objects as a source of reinforcement. First, Chisholm and Trowill (1971) have demonstrated that non-deprived stimulus-bound animals are sensitive to the taste qualities of the goal object under all levels of current intensity that reliably elicit the consummatory behavior. In that study, stimulus-bound drinkers experienced shifts in sucrose concentration (12% and 32%) at low, medium and high stimulation current intensity. In general, significantly large and consistent negative contrast effects were observed in the stimulus-bound animals across all current intensities following the 32% to 12% shift. The 12% to 32% shift elicited a somewhat smaller and less reliable positive contrast effect. Contrast effects in normal animals are often considered to be an

emotional response to changes in reward magnitude (Panksepp and Trowill, 1969). Therefore when stimulus-bound animals react in an emotional manner to shifts in reward magnitude it suggests that the goal object for stimulus-bound animals is also an important source of reinforcement.

The electrical stimulation as a source of reinforcement. Many studies have studied the role of neural control of reinforcement since the initial observation that rats would press a lever to deliver brief electrical shocks to their own brain (Olds and Milner, 1954). Experiments using self-stimulation rate as a measure of positive reinforcement have shown that the portion of the lateral hypothalamus bordering the medial forebrain bundle is the most positive area (Olds, Travis and Schwing, 1960; Olds, 1962). Electrodes that elicit stimulus-bound behavior are also located in this positive reinforcement area and animals will bar press to receive short pulses of electrical stimulation from the same electrodes that produce stimulus-bound behavior. However, the degree to which the full 30 seconds of stimulation typically used in stimulus-bound studies is positively reinforcing has not been fully tested.

The second purpose of this dissertation was to inves-

tigate the extent to which the electrical stimulation in stimulus-bound animals was reinforcing. Stimulus-bound subjects were placed in a shuttle apparatus and were allowed to choose between no electrical stimulation or a full 30 seconds of electrical stimulation at the same parameters that had previously elicited stimulus-bound behavior.

The response as a source of reinforcement. Glickman and Schiff (1967) have stressed the notion that the performance of a species-specific response sequence is reinforcing. It was concluded that the responses are reinforcing because they activate the underlying neural systems associated with reinforcement. Valenstein has recently applied a similar interpretation that emphasized the motor system and the reinforcement that is produced by the execution of a consummatory response to electrically-elicited behavior. This latest interpretation stated that the most important single source of reinforcement in stimulus-bound animals comes from the performance of the consummatory response. However, no direct measures of the reinforcement arising from the performance of a response have been made.

Since the specific nature of the goal object is a factor in maintaining the stimulus-bound behavior and

since the occurrence of the elicited consummatory response is usually confounded with the receipt of a goal object, the final purpose of this research was to investigate the incentive motivational value of a non-nutritive, non-hedonic goal object, namely a wood block which can be gnawed. Mendelson (1967) has reported that stimulus-bound drinkers bar pressed for electrical stimulation at a higher rate when water was available. Coons and Cruce (1968) reported similar results using food as the goal object. Here, a similar procedure was used to investigate the effects of the gnawing response on the bar press rate for stimulation which elicited the stimulus-bound response of gnawing.

EXPERIMENT 1

Effects of Previous Experience on Stimulus-Bound Behavior

Several experiments have attempted to manipulate response prepotency by manipulating environmental variables. First, Valenstein and Cox (1970) deprived animals of either food or water and stimulated them during the consummatory acts of eating or drinking. The results showed that neither the need state or the contiguity of eating or drinking with hypothalamic stimulation influenced the response pattern that emerged.

A second experiment used animals that displayed both stimulus-bound eating and drinking from the same electrode. The animals were then given two sessions per day during which they could display stimulus-bound eating in one chamber and stimulus-bound drinking in a distinctively different chamber. After 36 - 48 sessions the animals were given competitive tests with both food and water available simultaneously in both chambers. It was expected that the animals would learn to exhibit a specific behavior in a specific chamber and that this association would affect the results of the competitive tests so that stimulus-bound eating or drinking would occur more fre-

quently in the chamber previously associated with that behavior. The results showed that one behavior tended to dominate and to be exhibited more frequently in both chambers. Thus, it was concluded that experience with a goal object did not play a major role in controlling stimulus-bound behavior.

Although neither previous experience nor contiguity alone were sufficient to independently influence response prepotency, it may be possible to combine these manipulations so as to affect the form of stimulus-bound behavior that initially emerges. The previous attempts to affect stimulus-bound behavior have typically measured resistance to switching and have not maintained a strict contiguity between the electrical stimulation and the performance of the consummatory response. The degree to which previous experience influences response prepotency is of primary importance to the usefulness of the prepotency notion as an analytical tool in stimulus-bound behavior.

This experiment was designed to test the possibility that previous sustained experience with a consummatory response together with a strict contiguity between this response and the stimulation were sufficient to influence the type of stimulus-bound behavior that was eventually established. Specifically, animals were trained to drink a sucrose solution and the occurrence of the drinking was

paired with ESLH (ie. ESLH was contingent on drinking). Subsequent to this training, all animals were tested to determine if the previous experience with the contiguous relation between the drinking and the electrical stimulation influenced the probability or the form of the stimulus-bound behavior that emerged.

Method

Subjects

Ten Charles River albino rats approximately 90-100 days old were used. The animals were housed under constant lighting conditions and were allowed free access to food (Purina Lab Chow) and water in their home cages.

Surgery

Each rat was anesthetized with nembutal anesthesia (40mg./kg.) and bilaterally implanted with stainless steel monopolar electrodes (.40mm in diameter) insulated with Insl-X except for .5 mm at the tips. The electrodes were stereotaxically placed 0.8 mm posterior to bregma, 1.7 mm lateral to the midline and 8.9 mm below the top of the skull (Pellegrino and Cushman, 1967). The mouth bar was set 5 mm above the inter-aural line. A stainless steel screw attached to the skull served as the common electrode. Three jeweler's screws were attached to the skull so as to

form a triangle around the electrodes. The electrodes were secured to the screws and to the dry skull with Cranio-plastic cement (William Getz Co., Chicago, Illinois).

Apparatus

A 12 x 12 x 18 inch high fiber board box served as the experimental chamber. Two 7½ watt light bulbs and a 4 inch speaker delivering 70 db of white noise were located directly over the box. On one side of the chamber two metal drinking spouts approximately 5 inches apart and 3 inches above the floor were recessed in Plexiglas shields so that discrete tongue contacts could be recorded via electronic drinkometers (Grason Stadler, Model Nos. E4690A-1, E4690A-2). The presentation and recording of all events was fully automated through the use of conventional programing equipment.

The stimulation for all phases of the experiment was 60 cycle sine wave. A step-down transformer operated from a 110 volt A.C. line provided the electrical brain stimulation. Relatively constant current was obtained by placing a one megohm resistor in series with the animal. The current was regulated by an A.C. micropotentiometer and was continously monitored by a cathode ray oscilloscope (Tektronix, type 502A) placed in parallel with a 10,000 ohm resistor and an A.C. microammeter in series with

the animal.

Procedure

Pre-training. Five to seven days following surgery each animal was placed in the empty experimental chamber and was given 20 trials per day for 4 days during which it was exposed (in the absence of stimulation) to a two bottle choice situation consisting of water of a 12% w/w sucrose solution. Each trial was composed of a 30 second period during which the drinking tubes were introduced and a 60 second interstimulus interval during which the tubes were withdrawn. A cam-motor (BCS Machine and Mfg. Co.) was used to automatically insert and withdraw the tubes. Half of the animals always received the sucrose solution on the left side of the apparatus while the remainder of the animals received it on the right side.

Training and testing. During the 5 training days both the sucrose and the water spouts were presented and after the animal made 5 contacts with either tube the stimulation was switched on. Thirty seconds later the drinking tubes were withdrawn simultaneously with the offset of the stimulation. Each day during this phase of the experiment the current intensity was slowly increased until the drinking was disrupted as indicated by a tendency for the animal

to break contact with the tube for 2-3 seconds. Then the current intensity was immediately decreased by 2-3 microamps or until consistent drinking behavior was once again observed. In this way the electrical stimulation was maintained at its maximum effective intensity while the animal was drinking. Three large pellets (Purina Lab Chow) and a soft pine wedge 2 x 2 x 2 inches were placed in the chamber during training. Thirty 30-second trials with a 60-second interstimulus interval were presented each day. Following training all animals were given 5 days of testing during which all conditions remained the same as during training except that both the water and sucrose were continuously available. Thus the animals were tested to determine if the previous experience of drinking sucrose during ESLH would produce more stimulus-bound sucrose drinkers than gnawers, eaters, or water drinkers.

Histology

Following data collection the animals were sacrificed for histological verification of electrode placement. Each animal was given an overdose of nembutal anesthesia followed by perfusion with 10 percent formalin. The brains were frozen and 90 μ frontal sections were stained with

cresyl violet and mounted on glass slides.

Results

Histology

Figure 1 shows the area of the brain from which stimulus-bound behavior was elicited. In all cases the electrode tips were located in the lateral hypothalamus or zona incerta. The electrode sites that induced stimulus-bound behavior appear to overlap with the electrode placements reported by Valenstein et al. (1970).

Training

During the 4 days of pre-training, observations indicated that all animals learned to drink the sucrose solution for the full 30 second periods. When the ESLH was faded in during the drinking periods the response was not disrupted. Table I presents the mean lick rate per minute for the last 3 days of training. Although most animals sampled the water at some time during each daily session the dominant response concurrent with the ESLH was sucrose drinking.

Testing

The mean number of licks per minute which each animal

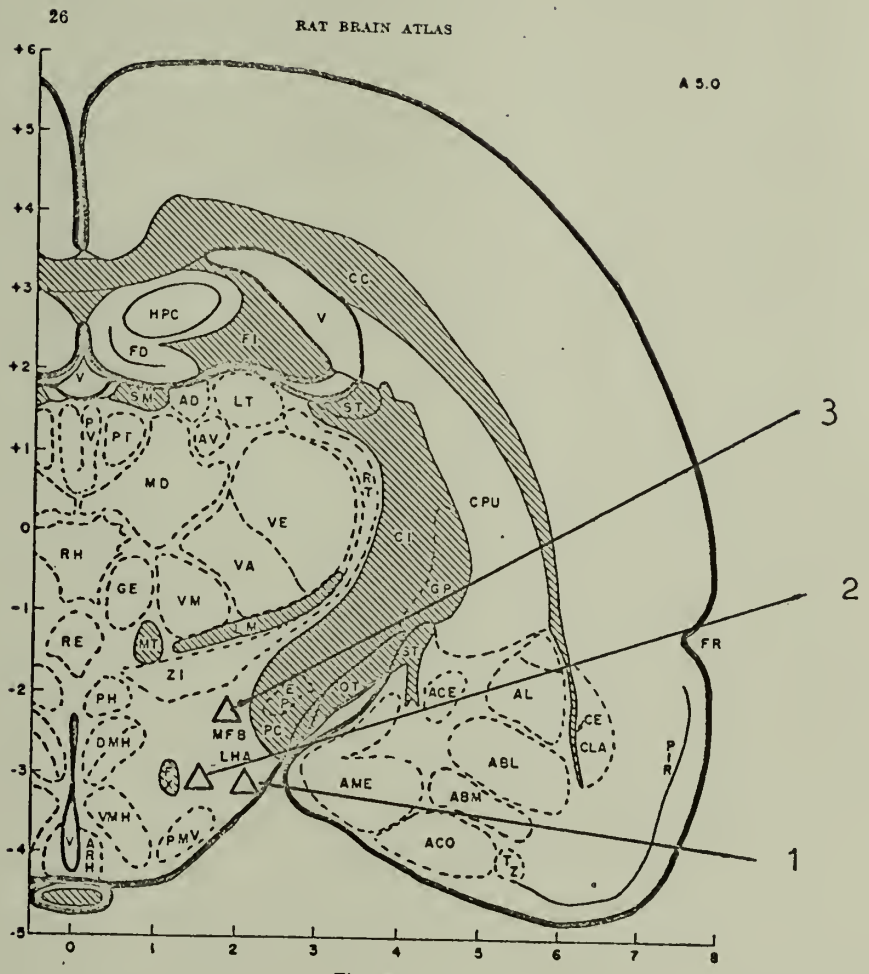

Fig. 16

Figure 1

Experiment 1, Summary of Histology

TABLE I

MEAN LICK RATE PER MINUTE FOR THE LAST THREE DAYS OF TRAINING

Subject No.	Day 3		Day 4		Day 5	
	water	sucrose	water	sucrose	water	sucrose
13	0.0	141.0	0.7	180.0	0.3	192.0
28	0.3	156.7	1.0	177.0	0.2	187.0
29	21.0	85.7	0.5	144.0	0.0	154.0
30	0.5	194.0	0.9	157.0	1.0	141.0
31	0.0	186.0	1.0	166.0	0.0	172.0
33	0.0	112.0	0.7	170.0	0.6	123.0
34	0.0	147.0	0.5	138.0	0.0	135.0
35	0.0	191.0	2.0	179.0	0.0	154.0
36	0.0	69.0	0.0	108.0	0.0	105.0
37	3.5	164.0	0.5	167.0	0.0	153.0

TABLE II

MEAN LICK RATE PER MINUTE FOR THE FIVE TEST DAYS AS A FUNCTION OF STIMULATION CONDITIONS

Subject No.	Stimulation	No Stimulation
13	128	146
28	142	134
29	74	92
30	62	92
31 G	150	118
33	86	104
34 D	264	18
35 G,E	140	170
36	78	86
37	140	168

Note: G = gnaw, D = drink, E = eat

made at the sucrose tube as a function of stimulation conditions is presented in Appendix A and Table II. It was expected that the previous experience of drinking sucrose in the presence of ESLH would increase the "prepotency" of the drinking response such that most of the animals would exhibit stimulus-bound drinking during testing. However, the only animal to display stimulus-bound drinking was No. 34.

Upon completion of testing it was possible that the low number of stimulus-bound drinkers was due to improper electrode placement rather than the failure of prior experience to affect stimulus-bound behavior. Thus, the nine animals which did not display stimulus-bound behavior were given seven more sessions in the testing situation. Although quantitative measures of eating and wood block gnawing were not available, close observations showed that subject No. 31 became a stimulus-bound wood gnawer and No. 35 consistently displayed gnawing and eating during the ESLH. These results verified the fact that an adequate implantation procedure and testing situation had been employed.

Discussion

The purpose of this experiment was to ascertain

whether the type of stimulus-bound behavior which initially emerges may be influenced by previous experience. The results showed that neither the experience with a consummatory response nor a strict contiguity between a response and ESLH was sufficient to influence the type of behavior which emerges.

Of critical importance to the above mentioned results is the fact that eventually 3 out of 10 animals (No. 31, 34, and 35) did display some type of stimulus-bound behavior. This 30 percent success rate is consistent with earlier work in this laboratory and with the success rate reported by Valenstein et al. (1969).

Other attempts to manipulate prepotency via environmental variables have also been unsuccessful (Valenstein and Cox, 1970). Although the present procedure produced only one stimulus-bound drinker out of three stimulus-bound animals it is interesting to note that the drinking response was the first to emerge. White, Wayner and Cott (1970) have reported that stimulus-bound gnawing and eating typically occur prior to drinking. Thus the drinking experience may have had some slight effect on the present data. However, it is difficult to see how such a weak effect could account for much of the control over stimulus-bound behaviors that emerge when a proced-

ure is used which lacks both specific previous experience with a response and a strict contiguity between the response and ESLH.

All data reported indicate that response prepotency cannot be manipulated by allowing the animal to have previous experience with the goal object. The less obvious procedures utilizing several weeks of experience with a response or possibly selectively breeding for certain stimulus-bound behaviors have not been attempted. However, these procedures would differ greatly from those procedures typically used in stimulus-bound research and the generalizability of the results would be questionable. Perhaps the most productive approach at this time would involve a reevaluation of what contributes to response prepotency. With the present inability to manipulate prepotency the usefulness of the notion is doubtful.

EXPERIMENT 2

Signaled and Self Regulated ESLH as a Source of Reinforcement in Stimulus-bound Animals

Many studies have shown that the area in the brain which elicits stimulus-bound behavior coincides with the area that is involved in electrical self-stimulation of the brain (Margules and Olds, 1962; Hoebel and Teitlebaum, 1962; Mendelson, 1967). In fact, Ball (1968) has reported that approximately 95% of the stimulus-bound eaters were also self-stimulators. Usually, however, stimulus-bound behavior is elicited by using a long (30 second) train of stimulation. On the other hand, self-stimulation is usually tested in a situation where the animal bar presses for relatively short (½ second) pulses. Therefore the degree to which the full 30 seconds of stimulation is rewarding is typically inferred from the results of experiments that use the short ½ second pulses.

More recently, Ball (1969) has concluded that hypothalamic stimulation that produces responses associated with hunger is <u>not</u> rewarding. The test of this involved delivering either a .5 second or a 5 second electrical stimulus and measuring the amount of milk intake during the stimulation. Then the animals were given a preference test in a Y-maze where they could run to either the .5 second

or the 5 second train of stimulation. The results showed that the animals consumed more milk during the 5 second trains, but preferred the .5 seconds of stimulation in the Y-maze when milk was not present. Experience with stimulus-bound animals has shown that it typically takes from 1 - 2 seconds for the stimulus-bound consummatory response to occur after the onset of stimulation. Thus an intake measure coupled with a stimulation period of .5 seconds would not reflect the extent to which an animal may be a stimulus-bound milk drinker. Furthermore, the fact that the rats preferred the .5 second stimulation does not support the conclusion that the full 5 seconds is not to some extent serving as a reward.

Other evidence indicates that some electrode placements in the lateral hypothalamic area produce both rewarding and punishing effects (Roberts, 1958; Olds, 1962; Valenstein and Valenstein, 1963; Hodos, 1965). Animals with electrodes in the parts of the brain that are both rewarding and punishing will press a bar to turn the stimulation on and after a few seconds make another response to turn the electrical stimulation off (Miller, 1960). Mendelson (1969) has demonstrated that an electrode with both positive and aversive effects may also elicit stimulus-bound feeding, drinking and gnawing. Therefore the affect-

ive nature of the electrical stimulation should be accurately assessed in stimulus-bound animals before one may determine the extent to which the electrical stimulation is reinforcing. Pilot data has shown that a shuttle apparatus is most useful in assessing the reinforcing role of the electrical stimulation of the brain in stimulus-bound animals since it provides a response that can be adopted by the animals without training.

Method

Subjects

Eighteen Charles River albino rats approximately 90-100 days old were used. The animals were housed under constant lighting conditions and were allowed free access to food and water in their home cages.

Surgery and histology

The surgical and histological procedures are the same as those used in Experiment 1.

Apparatus

A shuttle box 15 inches long, 10 inches wide and 18 inches high was the primary apparatus. The compartment was evenly divided by a 1 inch high hurdle. Two 7½ watt light

bulbs behind translucent Plexiglas shields and a 4 inch speaker were located directly over the box in such a way that both sides of the compartment received equal amounts of light and white noise. The floor was mounted on a pivot located beneath the hurdle. A microswitch was mounted beneath the frame such that the weight of the animal on one side of the box would close the microswitch. Conventional programing equipment was used to control the presentation of the stimulation and an Esterline Angus recorder monitored the position of the animal at all times.

Procedure

Screening. Seven days after surgery the animals were screened in the same apparatus used in Experiment 1. However, in this Experiment the subjects were given a choice of three goal objects; three large food pellets (Purina Lab Chow), water delivered via a metal drinking tube, and a wooden block 2 x 2 x 2 inches. If the initial behavior which emerged was stimulus-bound eating or gnawing the animal was allowed to exhibit this behavior for a maximum of 10 trials. The food pellets and wooden blocks were then removed from the chamber and the animals were given three 24 trial sessions with just the metal drinking tube present. The animals that were initially stimulus-

bound drinkers also received the three 24 trial sessions with just the water present.

Threshold determination. Following screening the animals that exhibited stimulus-bound drinking were given three ascending and three descending series of current intensities in order to determine the current intensity range through which the behavior would occur. The low-current level was the lowest level at which the behavior could be consistently elicited. The high-current intensity was the highest level possible without disruption of the behavior. A point midway between the high and the low levels was chosen as the medium current level.

Pre-training. Immediately after threshold determination all animals were given several days of training. Twenty-four 30 second trials with a 30 second interstimulus interval were presented each day. All three levels of current intensity were randomly utilized and minor adjustments in the current were made so that consistent, stable behavior would occur.

Testing. Following screening, each animal that had previously exhibited stimulus-bound drinking was placed on the left side of the shuttle box for a 30 minute adaptation session. During adaptation all equipment was activated

with the exception that no ESB was delivered. The following day each animal was placed on the nonpreferred side of the box for the 24 minute test session. When the animal moved to the stimulation side of the box the floor was depressed triggering the onset of the CS (houselights) and one second later the delivery of the ESB. The CS and ESB were delivered for a 30 second period. However, if the subject were to shuttle back to the non-stimulation side, then both the CS and ESB were immediately terminated. In this way, animals could quickly learn to control the frequency and duration of the ESB (ie. the rats could turn the stimulation on and off by jumping back and forth). If a rat remained on the stimulation side of the box for the full 30 seconds or more it would receive 30 seconds of stimulation with a 30 second interstimulus interval. All three levels of current intensity (low, medium and high) were randomly presented so that each animal received nine successive days of training at each level. The side of the apparatus where the stimulation was delivered was switched every three days forcing each animal to undergo two reversals within each 9 day period. The total time each animal spent on the stimulation side of the shuttle box and the duration of each stimulation were recorded.

Results

Histology

Histological verification of electrode placement was obtained from all animals and is presented in Figure 2. In all four cases the electrode tips were located within the lateral hypothalamus or the zona incerta in sites similar to those that have been reported by Valenstein et al. (1969).

Testing. Figures 3 - 6 show the amount of time each rat spent on the signaled ESB side of the shuttle box during each 24 minute session. The data are presented as a function of current intensity and the numbers on each plot represent the average stimulation train duration in seconds. It is apparent from the figures that all animals preferred the signaled, self regulated ESB side of the shuttle box and all animals relearned very rapidly following the reversals. Three of the four rats chose to receive an average stimulation train duration in excess of 20 seconds.

The mean amount of time on the signaled ESB side of the shuttle box is presented on Figure 7. In general, more than 75% of the time was spent on the signaled ESB side of the box. It is noteworthy that the rats spent a higher percentage of time on the signaled ESB side when

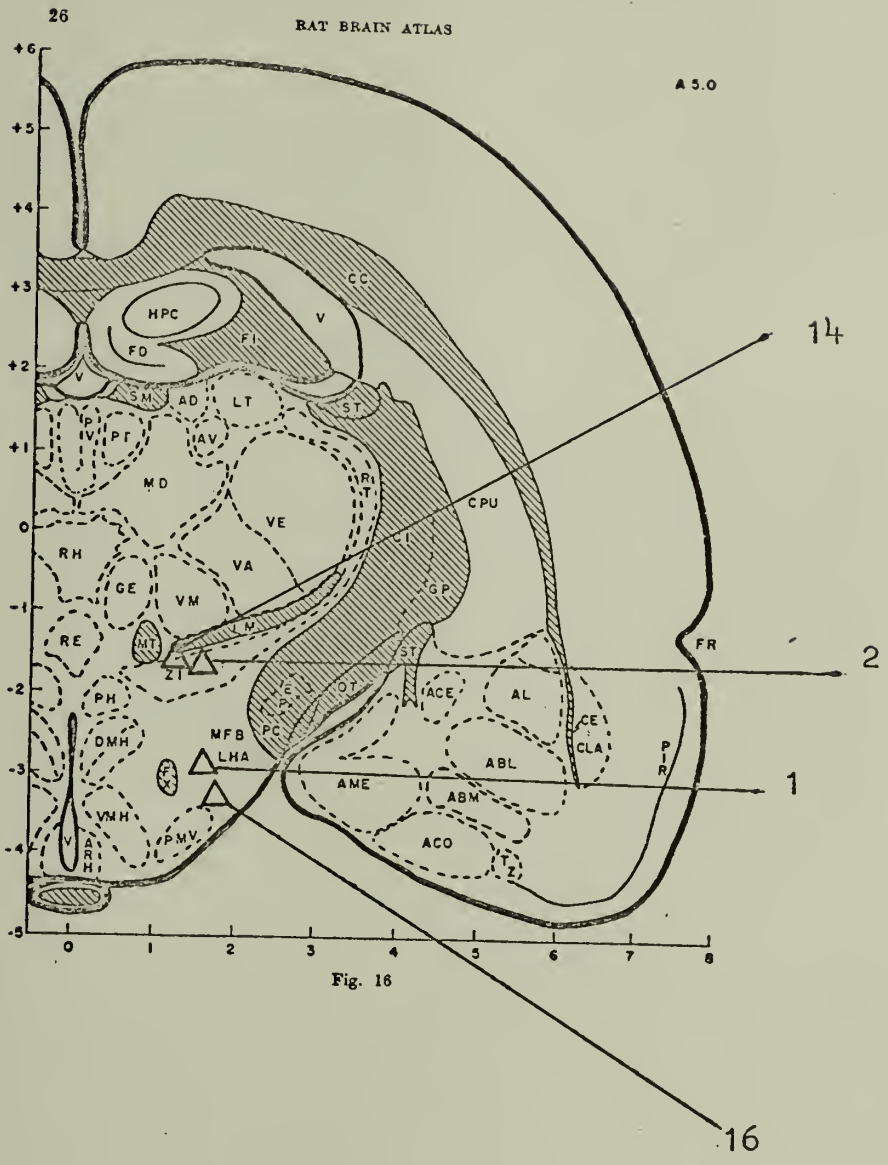

Fig. 16

Figure 2. Experiment 2, Summary of Histology

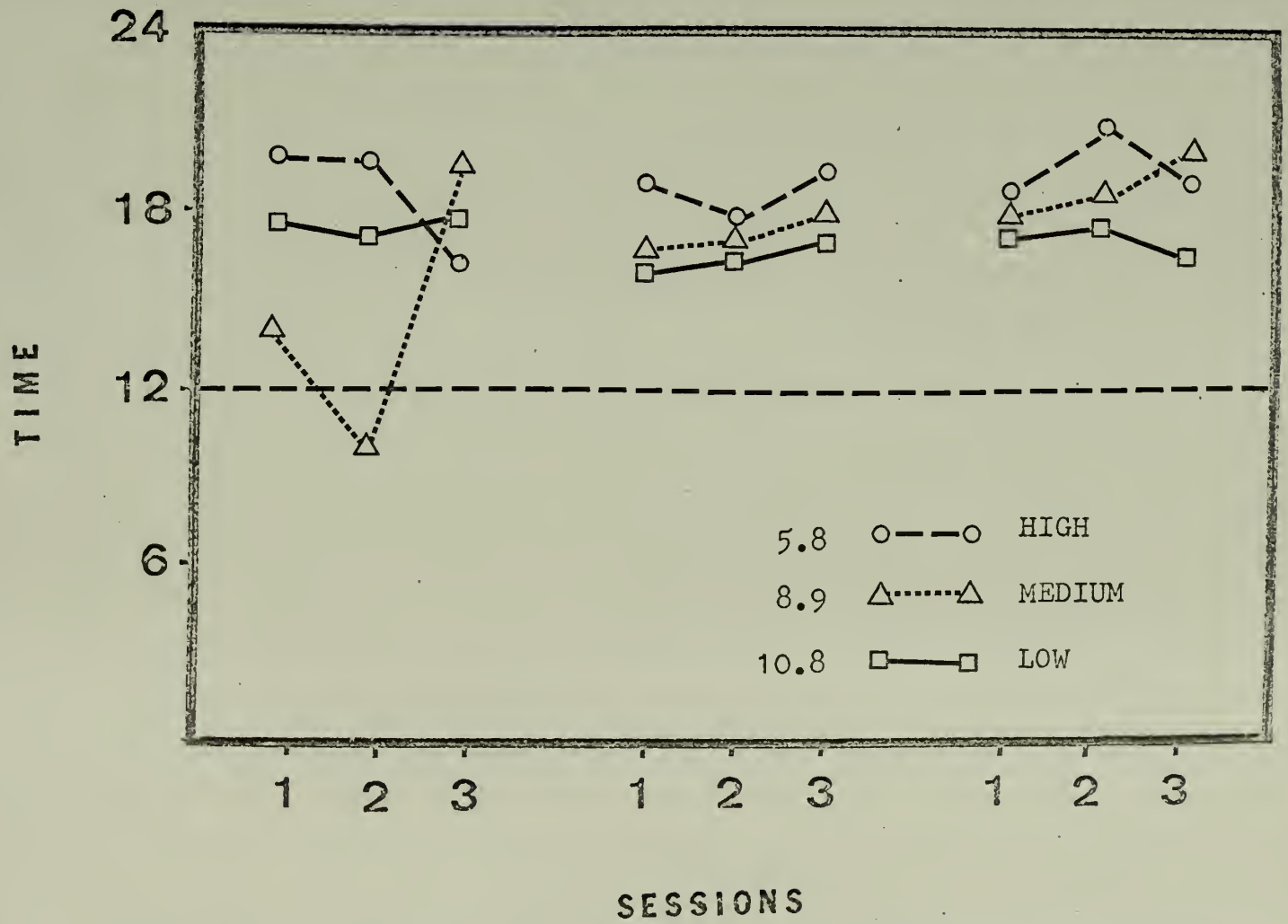

Figure 3. Experiment 2, Time in minutes spent on the signaled, self regulated side of the shuttle box for subject No. 1 as a function of current intensity. The numbers represent the average stimulation train duration (seconds) chosen at each current intensity level. The three groups of connected data points represent initial training and two reversals.

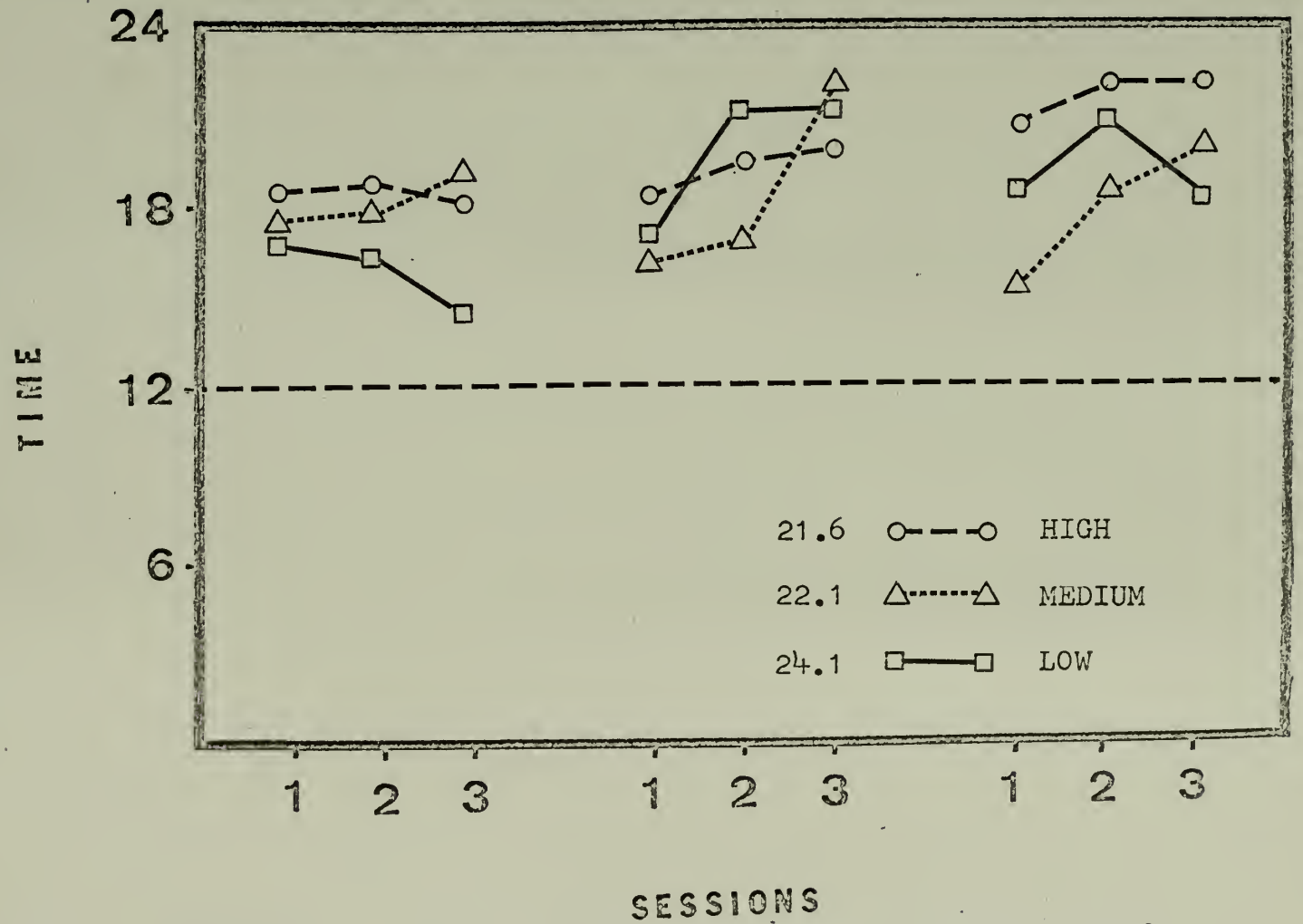

Figure 4. Experiment 2, Time in minutes spent on the signaled, self regulated ESB side of the shuttle box for subject No. 2 as a function of current intensity. The numbers represent the average stimulation train duration (seconds) chosen at each current intensity level. The three groups of connected data points represent initial training and two reversals

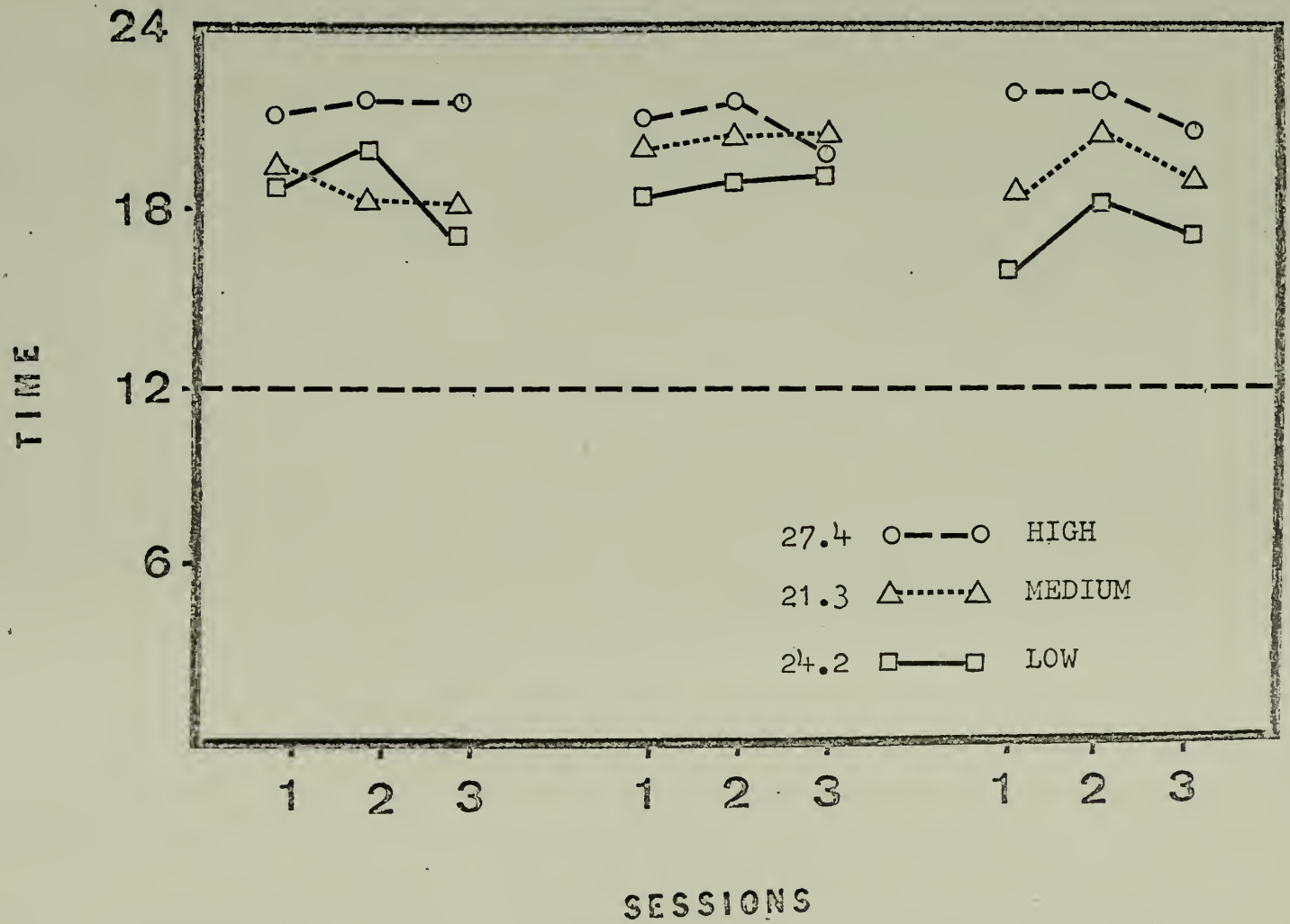

Figure 5. Experiment 2, Time in minutes spent on the signaled, self regulated ESB side of the shuttle box for subject No. 14 as a function of current intensity. The numbers represent the average stimulation train duration (seconds) chosen at each current intensity level. The three groups of connected data points represent initial training and two reversals.

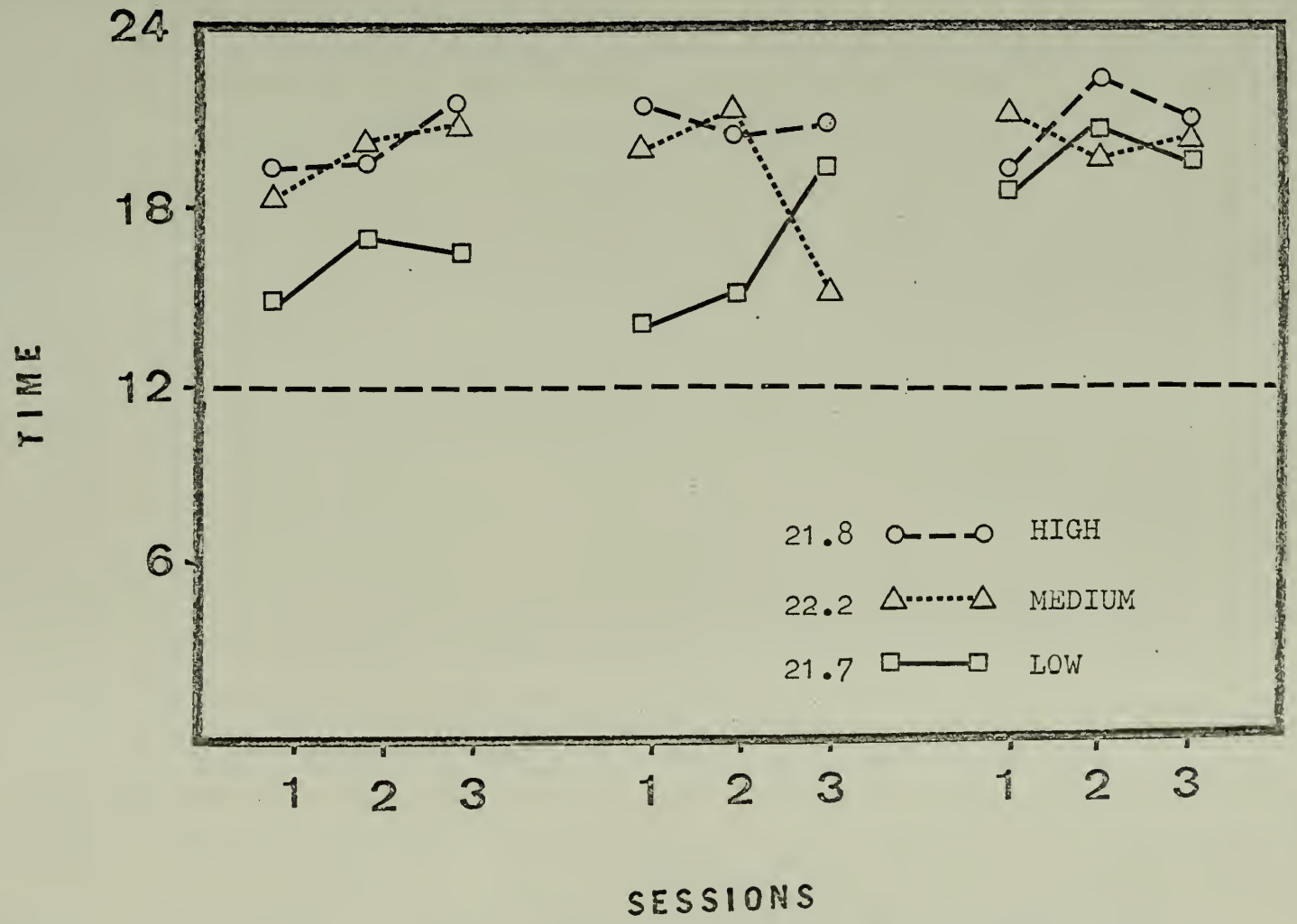

Figure 6. Experiment 2, Time in minutes spent on the signaled, self regulated ESB side of the shuttle box for subject No. 16 as a function of current intensity. The numbers represent the average stimulation train duration (seconds) chosen at each current intensity level. The three groups of connected data points represent initial training and two reversals.

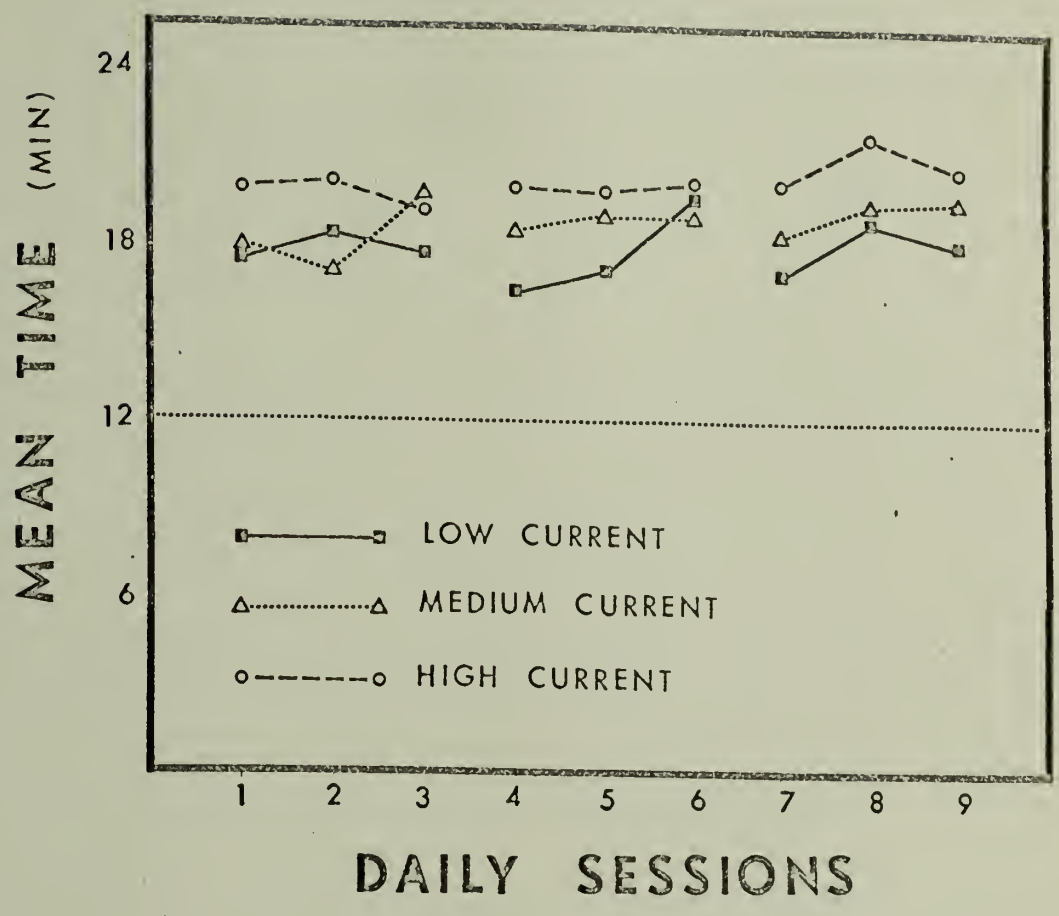

Figure 7. Experiment 2, The mean time spent on the signaled, self regulated ESB side of the shuttle box for all animals as a function of current intensity. The three groups of connected data points represent initial training and two reversals.

the high current was delivered than when the low current was delivered ($p < .032$).

Discussion

The major findings of this experiment were: (a) rats given a choice between signaled ESB at current intensities that previously elicited stimulus-bound drinking and no signaled ESB choose to receive the stimulation; and (b) high current intensities did not adversely affect the choice and in general the duration of ESB chosen was directly related to the stimulation intensity.

The fact that rats chose to receive signaled ESB at the same intensity that elicited stimulus-bound drinking tends to support the notion that the stimulation is a potential source of positive reinforcement in the stimulus-bound situation. However the test environment differed in two critical ways from the stimulus-bound situation. First, the occurrence of the ESB was signaled by the onset of the houselights. Cantor and LoLordo (1970) have shown that rats prefer signaled ESB (0.5 second bursts delivered on a VI 60 second schedule) when given a choice between signaled and unsignaled brain stimulation. Thus the actual stimulation train durations may have been more rewarding due to the presence of the signal in this study.

Second, Steiner, Beer and Shaffer (1969) have demonstrated that rats escape from their own prerecorded self-stimulation patterns. This suggests that the stimulation becomes aversive when the animal cannot control the schedule of delivery. Therefore a test of the rewarding properties of the electrical stimulation in stimulus-bound animals that utilizes a procedure that does not allow the animal to control the presentation of the ESB might produce somewhat different results. Experiment 2 was designed to investigate this possibility.

EXPERIMENT 3

Unsignaled and Non-self Regulated ESLH as a Source of Reinforcement in Stimulus-bound Animals

In order to more accurately test the rewarding properties of electrical stimulation in stimulus-bound behavior a procedure has been developed so that animals choose either no stimulation or the exact stimulation that has previously been used in stimulus-bound training. The primary apparatus was a shuttle box without any of the appropriate goal objects.

Method

Subjects

Fifteen male Charles River albino rats approximately 100 days old were used. The animals were housed under constant lighting conditions and were allowed free access to food and water in their home cages.

Surgery-histology and apparatus

The surgical-histological procedures and apparatus were the same as those reported in Experiment 2.

Procedure

Screening. Seven days after surgery the screening procedure was carried out in the same apparatus as used in Experiment 1. The screening procedure was the same as that used in Experiment 2 with the exception that after the emergence of a specific response a series of two 20 trial sessions were run with just the originally chosen goal object present. The stimulation was presented for 30 seconds with a 30 second interstimulus interval and the current intensity was adjusted so that the animals received the minimum current required to consistently produce the behavior.

Testing. Following screening each animal that had previously exhibited stimulus-bound behavior was placed on the left side of the shuttle box for a 60 minute adaptation session. During adaptation all equipment was functioning; however, the electrical brain stimulator was not turned on. The day after adaptation each animal was placed in the apparatus for a 60 minute testing session. The side of the shuttle box on which the animal activated the electrical stimulation circuit was opposite to the preferred side as indicated by the adaptation session. When the animal moved to the stimulation side of the box the floor was depressed and the animal received ESLH at the same current intensity and on the same fixed interval (FI) 30

second schedule that was used during screening. If an animal shuttled back to the non-stimulation side the FI schedule did not advance. However, once a 30 second ESB period was activated it ran to completion irrespective of the subject's position in the apparatus.

The total time of stimulation each rat received and the amount of time spent on the stimulation side of the shuttle box was recorded. After 6 days of testing the side upon which the stimulation was delivered was switched to insure against a position preference. After the stimulation side was reversed all animals were tested for 3 more days.

Results and Discussion

The localization of the electrode tips for the four animals which displayed stimulus-bound behavior is indicated in Figure 8. In all cases the electrodes were in the lateral hypothalamic area.

The percentage time spent on the unsignaled, non-self regulated ESB side of the shuttle box for each animal is presented in Figures 9-12. In general there were no consistently strong preferences or aversions to the ESB. The results of the adaptation session showed that biases created by the experimental environment were minimal due

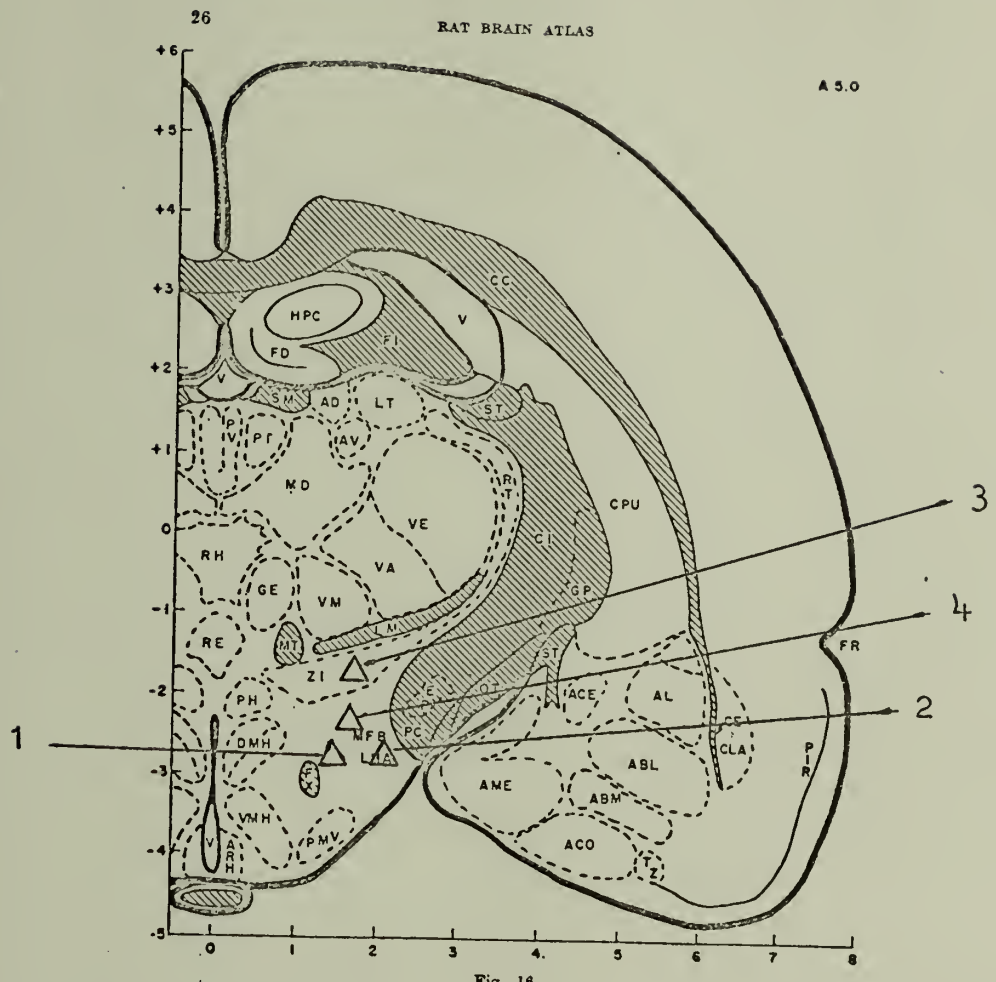

Fig. 16

Figure 8

Experiment 3, Summary of Histology

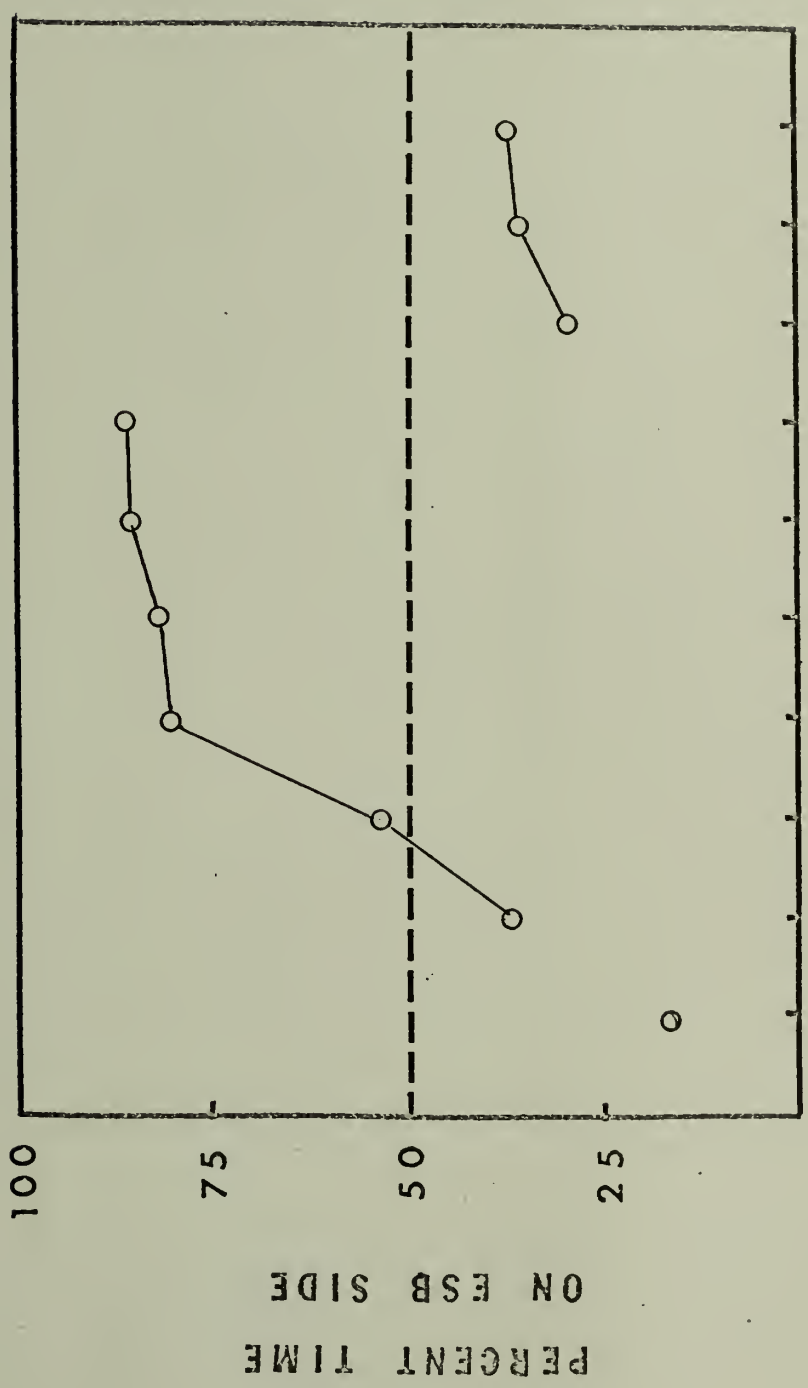

Figure 9. Experiment 3. Percentage time on unsignaled, non-self regulated ESB side of the shuttle box for subject No. 1. The first data point represents the side preference in the absence of ESB. The two groups of connected data points represent initial training and one reversal.

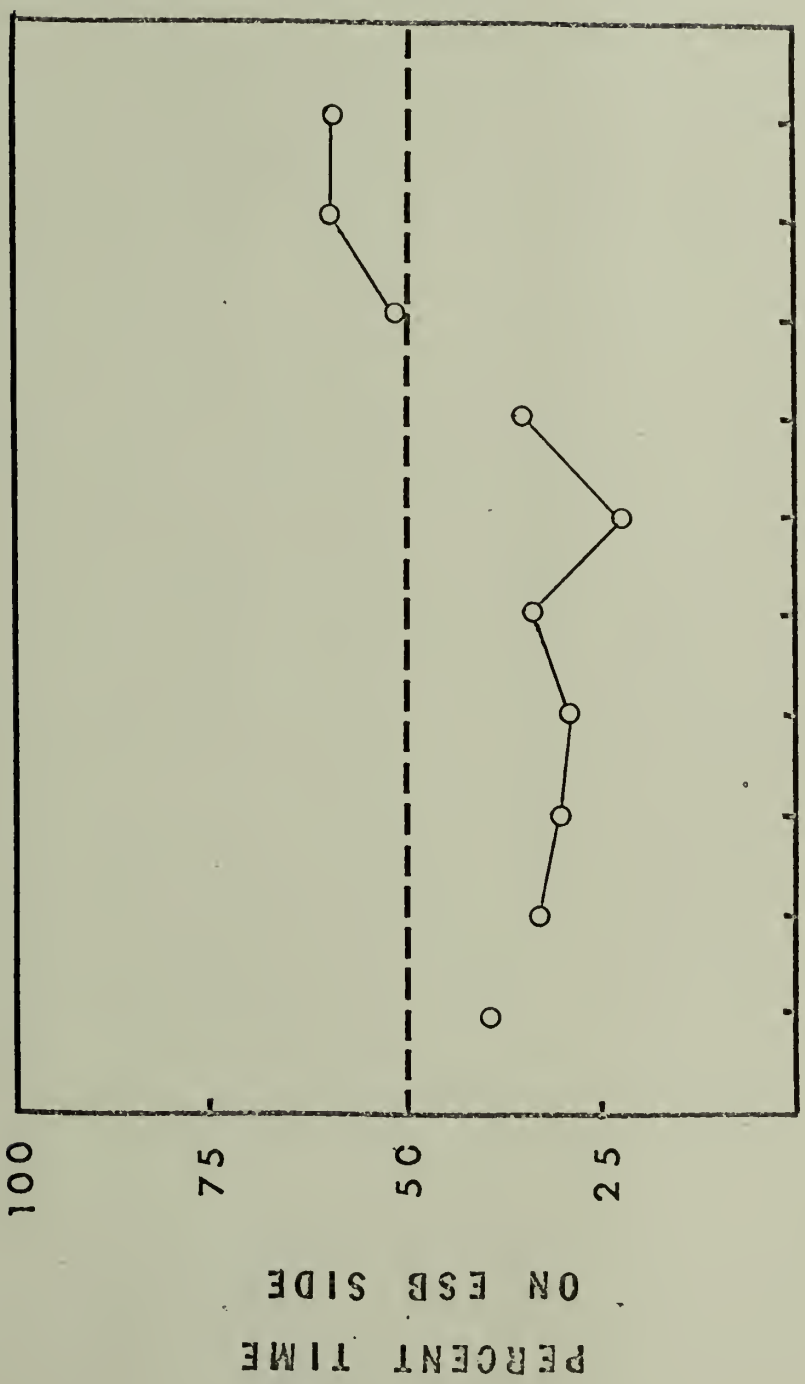

Figure 10. Experiment 3, Percentage time on unsignaled, non-self regulated ESB side of the shuttle box for subject No. 2. The first data point represents the side preference in the absence of ESB. The two groups of connected data points represent initial training and one reversal.

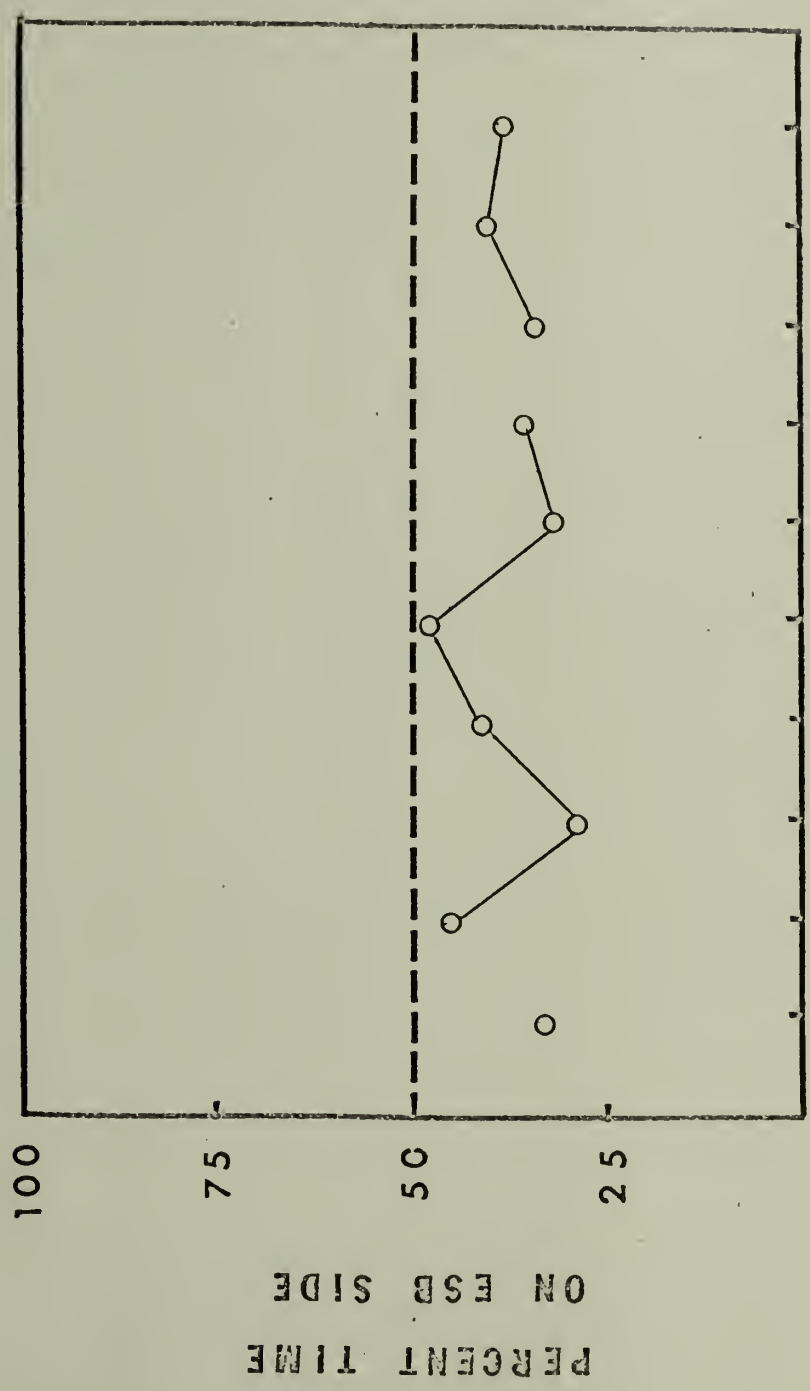

Figure 11. Experiment 3, Percentage time on the unsignaled, non-self regulated ESB side of the shuttle box for subject No. 3. The first data point represents the side preference in the absence of ESB. The two groups of connected data points represent initial training and one reversal.

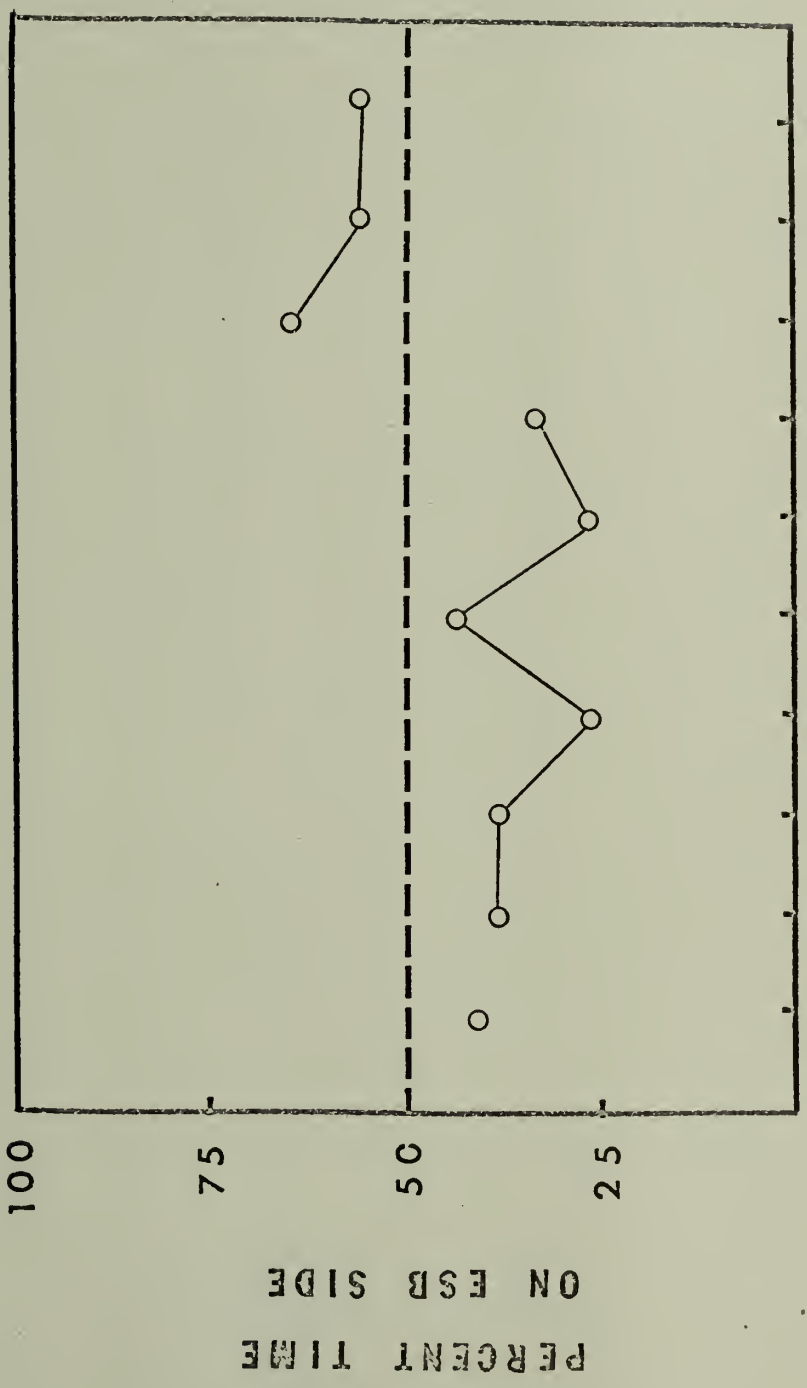

Figure 12. Experiment 3, Percentage time on the unsignaled, non-self regulated ESB side of the shuttle box for subject No. 4. The first data point represents the side preference in the absence of ESB. The two groups of connected data points represent initial training and one reversal.

to the fact that subject No. 1 and 3 preferred the left side while Subject No. 2 and 4 preferred the right side. The ESB side during the original training was opposite to the animal's preference indicated in the adaptation session. It was expected that the positive qualities of the ESB would attract the rat away from the original position preference. If the ESB were aversive, then the preference during initial training would coincide with the adaptation preference. However, in each animal whether the affective quality of the ESB was positive or negative, the preference during training and the reversal should have remained consistently above or below the 50 percent level. This result was found only in subject No. 3 where a small but consistent aversive affect was recorded. The responses of subjects 1, 2 and 4 indicated that factors other than the ESB were controlling their behavior. The results of Experiment 2 which was run in the same apparatus and the lack of a consistent side preference during adaptation suggests that these data are probably best explained by a weak ESB effect rather than a strong positional bias.

The only cue available to the animal for making the side discrimination was stimulation onset. Once the stimulation was initiated the duration was a full 30 seconds irrespective of the animal's position in the shuttle box.

Due to the fact that the ESLH produces forward moving searching behavior the animal typically wandered from side to side in the shuttle box during the stimulation period and exhibited many intervening activities. These intervening activities and the fact that the animal received the ESB on both sides of the shuttle box probably masked the relationship between stimulation onset and the animal's position in the box at the time of stimulation onset.

EXPERIMENT 4

Unsignaled and Self Regulated ESLH as a Source of Reinforcement in Stimulus-bound Animals

The results of Experiment 2 have shown that if stimulus-bound animals are given a choice between no ESB and signaled ESB in a situation where the frequency and duration of the stimulation can be self regulated, then all animals remain on the stimulation side of the shuttle box approximately 75 percent of the time. However, the results of Experiment 3 suggest that either the unsignaled, non-self regulated delivery of ESB is not rewarding, or that the animals did not have enough information (even after 8 days of training) to solve the two choice task.

The purpose of this experiment was to examine more closely the sources of reinforcement in the signaled, self regulated ESB preference situation. Other researchers have reported that both the warning signal (Cantor and LoLordo, 1970) and the control over the delivery of ESB (Steiner, Beer and Shaffer, 1969) are important sources of reinforcement. Due to the fact that the ESB is usually not signaled in the stimulus-bound situation, just the opportunity for an animal to control the rate and duration of the brain stimulation was manipulated.

Method

Subjects

The eight stimulus-bound animals from Experiment 2 and 3 were used. The 4 rats from Experiment 2 were run at the medium current intensity and the 4 rats from Experiment 3 were run at the stimulus-bound thresholds used in Experiment 3.

Apparatus and testing procedures

The apparatus and procedure was the same as in Experiment 2 except that the houselights were on at all times and were not used as a CS. The 4 animals run at medium current intensity underwent 5 days of acquisition and 5 days of reversal training while the 4 animals run at low current intensity had 3 days of acquisition and 3 days of reversal training.

Following day 6 the 4 animals from Experiment 3 were run through a second replication of the design. However, this time a CS (offset of the houselights) was introduced at the same parameters used in Experiment 2. The light-off CS was used to control for the possibility that the light-onset used in Experiment 2 was reinforcing.

Results

The mean amount of time on the unsignaled ESB side of the shuttle box for the 4 animals that received medium current intensity is shown in Figure 13. The mean percentage of time spent on the ESB side for the last three days of acquisition and reversal was 67 and 57 percentage respectively. The individual data in Appendix B show that all animals run at the medium current intensity preferred the ESB side during initial training and that all animals slowly showed a preference for the ESB by the last day of reversal training.

The mean time on the ESB side for the rats run at the stimulus-bound current intensity threshold is shown in Figure 14 and Appendix B. In general, the animals had large individual differences and no consistent pattern of responding emerged. The ESB appeared to have an aversive effect on subject No. 2 and 3 as they spent more time on the non-stimulation side. However, the effect of the stimulation on subject No. 1 and 4 was minimal and a side preference developed during initial training and was carried into the reversal sessions.

Following the last day of reversal the 4 animals that did not show a preference for the low intensity ESB were retested with a CS present. As evident in Figure 15

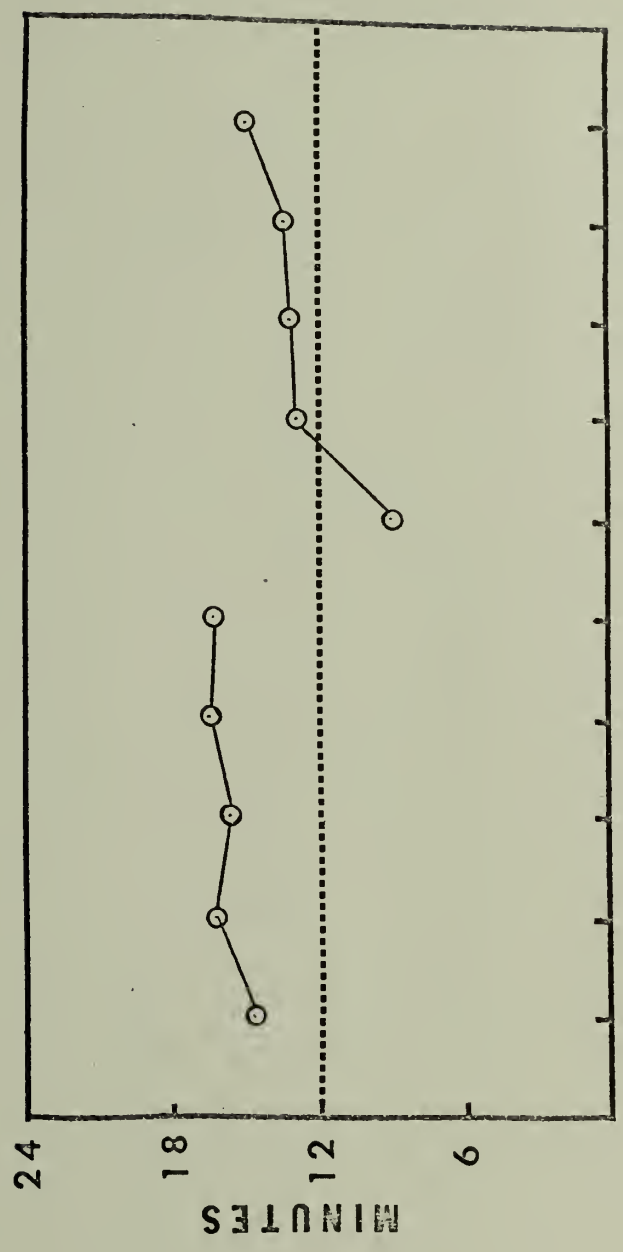

Figure 13. Experiment 4. Mean time spent on the unsignaled, self regulated ESB side of the shuttle box for the four subjects that received medium current intensity. The two groups of connected data points represent initial training and one reversal.

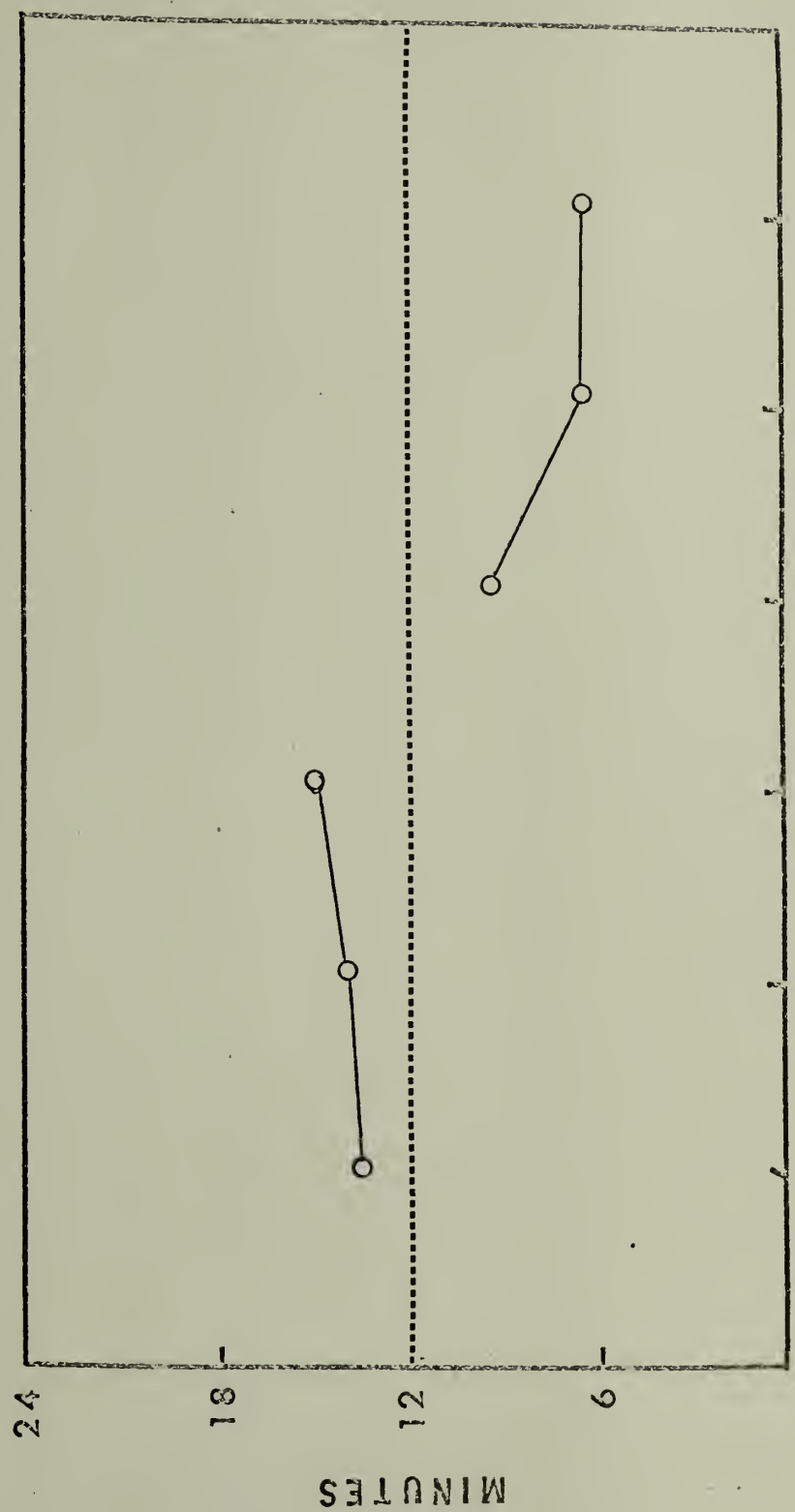

Figure 14. Experiment 4, Mean time spent on the unsignaled, self regulated ESB side of the shuttle box for the four subjects that received low current intensity. The two groups of connected data points represent initial training and one reversal.

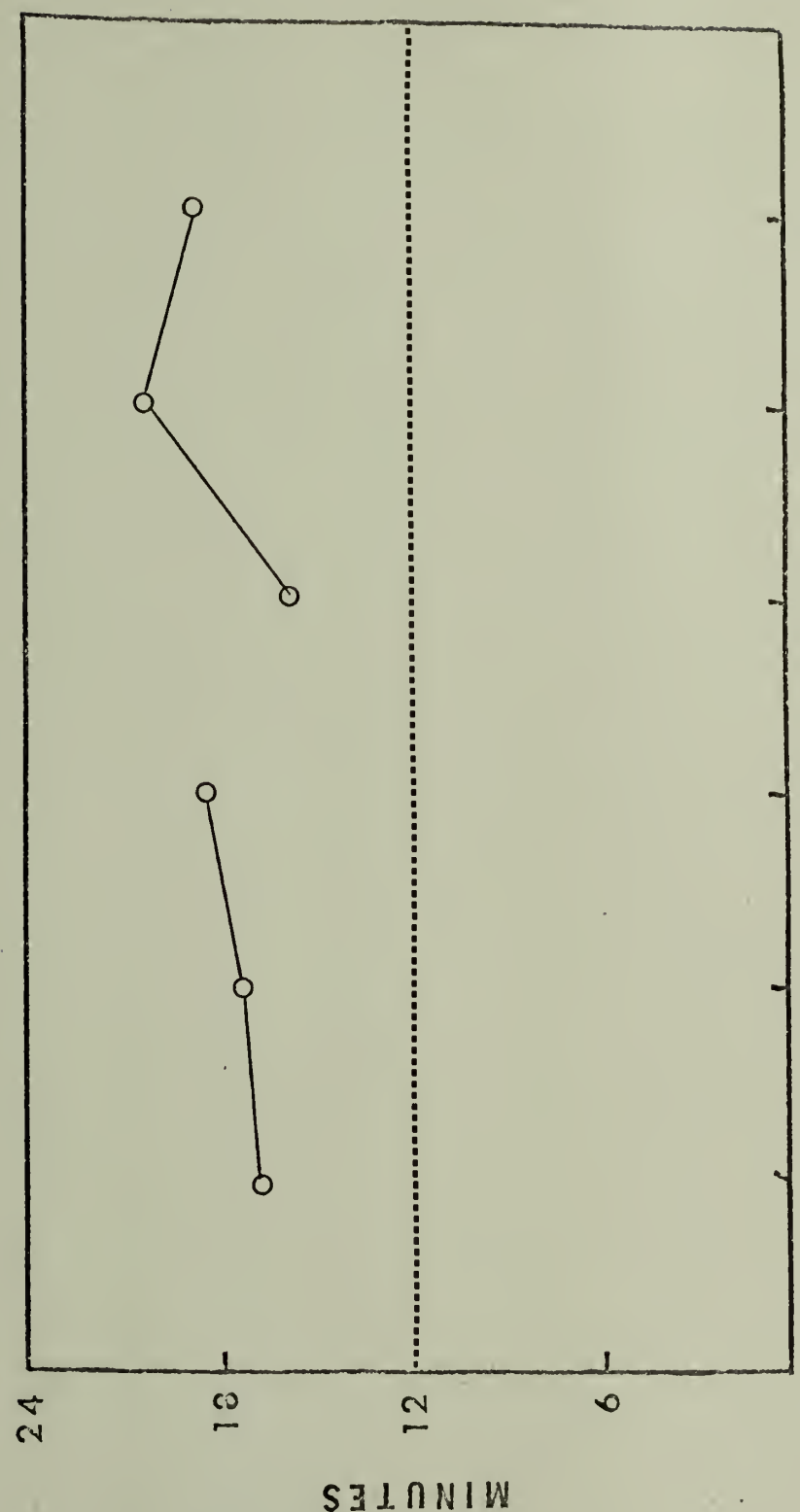

Figure 15. Experiment 4, Mean time spent on the signaled, self regulated ESB side of the shuttle box for the four animals that received low current intensity. The two groups of connected data points represent inital training and one reversal.

there was a preference for the signaled, self regulated ESB. However, this effect was produced by subjects No. 1, 2, and 4. Animal No. 3 tended to avoid the stimulation. The average pulse train duration for each animal showed that the rats which preferred the ESB also preferred long pulse train durations (Appendix B).

Discussion

The results of this study confirm the earlier finding that long durations of signaled ESB in stimulus-bound animals is rewarding. However, the data concerning the affective aspects of unsignaled ESB is less clear. The data are generally consistent with the notion that supra stimulus-bound threshold intensities of ESB are slightly rewarding while intensities close to threshold produce weak and conflicting results.

The lack of any consistent trend in the data obtained from the stimulus-bound animals run at current intensities close to threshold is not surprising when the results of Coons and Gruce (1968) are considered. In that study it was found that current intensities near threshold are reinforcing for stimulus-bound animals only when the appropriate goal object is present.

EXPERIMENT 5

The Performance of the Consummatory Response as a Source of Reinforcement in Stimulus-bound Animals

Valenstein, Cox and Kakolewski (1970) have emphasized the importance of the consummatory response in stimulus-bound behavior. In general, the motor system analysis of species specific response sequences suggested by Glickman and Schiff (1967) has been applied to stimulus-bound behavior. It is maintained by Valenstein et al. (1970) that the execution of the consummatory response is immediately reinforcing and that this reinforcement is independent of the incentive properties of the goal object or of any subsequent biological consequences.

Several studies may be cited in apparent support of the notion that the performance of the consummatory response is an important source of reinforcement in stimulus-bound behavior (Coons and Cruce, 1968; Mendelson, 1966,1967,1969; Mogenson and Morgan, 1967; Phillips and Mogenson, 1968; Phillips, Cox, Kakolewski and Valenstein, 1969; Valenstein et al., 1970). However, in most cases the studies were designed to investigate the motivational aspects of ESB and precise statements concerning reinforcement are not possible. First, Mendelson (1966) has shown that stimulus-

bound rats prefer the combination of food and brain stimulation to brain stimulation alone. In another study (Mendelson, 1967) it has been shown that stimulus-bound rats would only bar press for 5 second bursts of ESB if water was available. Thus the combination of ESB and water was preferred to ESB alone. But in both of these studies one cannot determine whether the incentive qualities of the goal object, the performance of the consummatory response, or some combination of these factors was the source of reinforcement.

More recently, Phillips et al. (1969) have utilized a procedure involving object carrying in a shuttle box. Rats were trained to self-stimulate by shuttling back and forth. Then small edible and inedible objects were introduced and they were picked up and carried to the non-stimulation side of the chamber. When the objects were present the self-stimulation rate increased; however, the duration of the stimulation pulses decreased. There is some evidence that long durations of ESB are not as rewarding as shorter durations (Keesey, 1964; Beer, Steiner and Shaffer, 1968; Mendelson, 1969). Thus in the object carrying experiment the reinforcement arising from the performance of the response is confounded with the animal's preference for shorter durations of stimulation.

One approach that could be used to separate the goal object from the performance of the response as a source of reinforcement would be to use intra-gastric fistula preparations. The difference in bar press rate between stimulus-bound animals pressing to receive intragastric injections and animals executing the consummatory response would be some indication of the degree to which the response is reinforcing. However, Gandelman (1969) in using this procedure to analyze the role of oral pharyngeal factors in the control of eating elicited by direct chemical stimulation (norepinephrine) of the lateral hypothalamus, observed that animals during intragastric feeding also perform mouth movements similar to those that occur during the consummatory act of eating.

In this experiment it was decided to shift to a new response, gnawing. The animals were trained to press a bar for 3 seconds of ESLH. Subsequent tests of the bar press rate with and without wood blocks available reflected whether the performance of a gnawing response was reinforcing to stimulus-bound animals.

Method

Subjects

Twenty Charles River male albino rats weighing 300-

400 grams (80-100 days old) were used. All animals were housed under constant lighting conditions and were allowed free access to food and water in their home cages.

Surgery and histology

Bipolar stainless steel electrodes (size MS-303-0.18) from the Plastics Products Co. were unilaterally implanted in animals that were anesthetized with nembutal anesthesia (40mg./kg.). The electrodes were insulated except for the cross-section of the wires at the tips. Owing to the low (30%) occurrence of stimulus-bound behavior in the previous experiments the procedure used by White, Wayner and Cott (1970) was used here. The mouth bar was positioned such that bregma and lamda were in the same horizontal plane. The electrodes were placed 3.0 mm posterior to bregma, 1.35 mm lateral to the midline and 8.25 mm ventral to the top of the skull. The remainder of the surgical and histological procedure was the same as in Experiment 1.

Apparatus

Two identical Plexiglas boxes 9 x 10 x 11 inches high were used as experimental chambers. A lever was mounted 1.25 inches above the floor at one end of each box. Holes were drilled such that water bottles could be mounted 1.5

inches to either side of both bars and 2 inches above the floor. Two 7½ watt light bulbs shielded with translucent Plexiglas and a 4 inch speaker delivering 70 db of white noise were located directly over the chamber. Conventional electromechanical equipment was used to control the presentation of the ESB and to record the bar press responses. The 60 cycle sine wave stimulation was generated by the stimulator utilized in Experiment 1.

Procedure

Screening and threshold determination. After a 5 day post operative recovery period each animal was placed in one of the chambers and screened for the presence of stimulus-bound behavior. Three food pellets (Purina Lab Chow), two wooden blocks 2 x 2 x 2 inches and two water bottles with metal drinking spouts were available in the box. The electrical stimulation was delivered for 30 seconds with a 30 second period between presentations. Gradually, the current was increased from zero level in 3 microamp steps until a forward moving searching behavior was observed. The animal was then stimulated until some stimulus-bound behavior emerged. Coons and Cruce (1968) have shown that a three second stimulation deviation was suitable to produce a good bar press rate for ESLH and consistent

stimulus-bound behavior. Therefore once a stimulus-bound behavior occurred, the stimulation duration was reduced to three seconds and an ascending and descending series of current intensities was used to establish the minimum current needed to elicit the response.

Training and testing. Each animal that exhibited stimulus-bound behavior was trained to bar press for supra-threshold 3 second trains of ESLH delivered through the same electrode that induced the stimulus-bound behavior.

A daily testing session consisted of 8 two minute trials in each of the two experimental chambers. The chambers were identical except that one box contained the appropriate goal object (food pellets, wood blocks or water). At the beginning of each trial the animal was placed in the middle of the alternate box. The presence or absence of goal objects was counterbalanced to control for order effects and each day the box containing the goal objects was varied to control for position preference.

Results

Histology

The 6 stimulus-bound animals that were used in testing were sacrificed and perfused with 10 percent formalin.

The brains were then cut in 90 μ sections, stained with cresyl violet and mounted on glass slides. An examination of electrode placement shown in Figure 16 indicated that the electrode tips were located in the lateral hypothalamic area. These placements are similar to those used in previous reports and those reported by Valenstein et al. (1969).

Screening and training

Five out of the 18 rats screened exhibited stimulus-bound eating, drinking or gnawing. Rat No. 31 that had displayed stimulus-bound gnawing at the end of Experiment 1 was added to the experimental group to form a total of 6 subjects. All 6 animals quickly learned to bar press for ESLH at current intensities 1-7 microamps above the stimulus-bound threshold. Table III presents the minimum current intensity needed to elicit stimulus-bound behavior and the current intensity required to maintain bar pressing for ESLH that elicits stimulus-bound behavior. In all cases the minimum intensity required to produce self-stimulation in the presence of the appropriate goal object was higher than the threshold for stimulus-bound behavior ($p < .032$, two tailed sign test). Also included in Table III is the current intensity used during screening

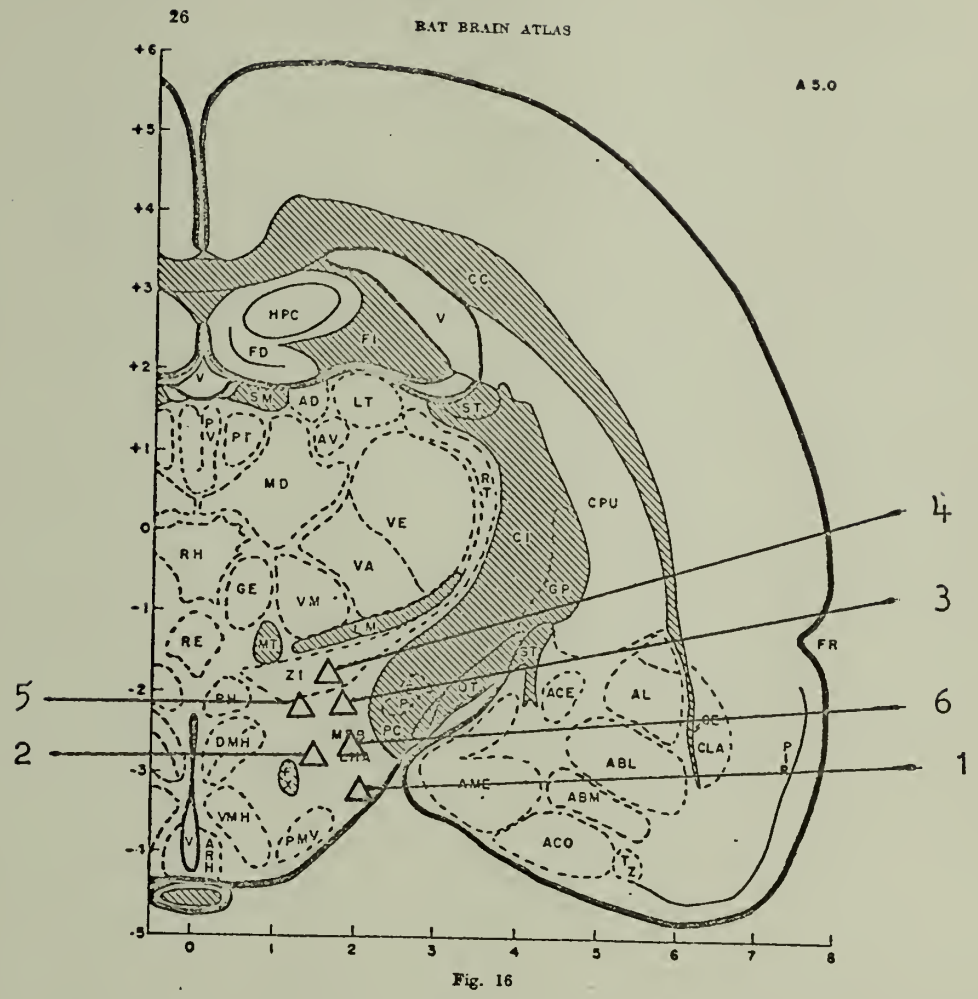

Fig. 16

Figure 16

Experiment 5, Summary of Histology

TABLE III

CURRENT INTENSITY IN MICROAMPERES*

Subject No.	Screening	Stimulus-bound Threshold	Self-stimulation Threshold
31G	20	13	17
47D	28	17	24
53D	15	12	15
76G	13	6	11
77E	8	3	5
79D	11	3	4

*Note: G = gnaw, D = drink, E = eat

to initially elicit stimulus-bound behavior. This current intensity was determined during screening by slowly increasing the current until the typical "forward moving searching behavior" was observed (Valenstein et al., 1969). A post hoc comparison showed that in every case the current intensity used initially to induce stimulus-bound behavior was equal to or higher than the self-stimulation threshold. This finding is consistent with the view that the positive reinforcement from the ESLH helps shape the initial stimulus-bound behavior.

Testing

Table IV and Appendix C show the mean bar presses per day for all 6 rats as a function of the availability of the appropriate goal object. All animals showed a higher bar press rate when interaction with a goal object was possible than when the goal object was not available ($p < .032$ by a sign test). The mean bar press rate for the two stimulus-bound gnawers in the presence and absence of the wood blocks were 402 and 152 respectively. These scores compare favorably with the 389.7 responses emitted with goal objects available and 128.2 responses with no goal objects available that were emitted by the rats consuming water or food.

TABLE IV

TOTAL BAR PRESSES PER ANIMAL FOR THE 4 TEST DAYS AS A FUNCTION OF OBJECT AVAILABILITY

Subject No.	Goal Objects Available	Goal Objects Not available
31G	497	131
47D	350	209
53D	527	124
76G	307	173
77E	241	135
79D	441	45

Note: G = gnaw, D = drink, E = eat

Observations confirmed that all animals made contact with the goal object when they received ESLH. Quantitative data are not available from the stimulus-bound gnawers or eaters, however intake volume over the last 2 testing days for the stimulus-bound drinkers is presented in Appendix C. The average volume of water consumed per session was 14.3 cc. This volume was consumed exclusively during stimulation periods due to the fact that stimulation offset produced response inhibition similar to that reported by Cox, Kakolewski and Valenstein (1969).

Data were also collected which measured the amount of time between placement of the animal in the chamber and the occurrence of the first bar press response (Appendix C). Four out of the six animals had consistently longer bar press latencies in the absence of the appropriate goal object. The mean bar press latency during the last two test days for all animals without goal objects was 42.0 seconds and when goal objects were present the latency was 22.6 seconds.

DISCUSSION

The results of this study demonstrate that stimulus-bound animals bar press for 3 second trains of ESLH at a higher rate when they are able to gnaw on wood than when wood is not available. The differential bar press rate

compares favorably with the rates of other animals that consume food or water during ESLH. This result is surprising if one considers the fact that at the end of a 3 second stimulation period the stimulus-bound drinkers are in the immediate vicinity of the bar while the stimulus-bound gnawers are frequently left on the opposite side of the box. Often, stimulus-bound gnawers display forward searching behavior in the presence of ESLH and do not go directly to the wood block. The gnawing is emitted only after the searching behavior eventually brings the animal in contact with the goal object. In contrast to this behavior, stimulus-bound animals that bar press for 3 second trains of ESLH return directly to the bar in a "purposeful manner" after interaction with the goal object. However, on trials where the ESLH terminated prior to contact with the goal object the next bar press often occurred only after the animal's normal searching behavior brought him into the vicinity of the bar. Thus with stimulus-bound drinkers the interaction with the goal object kept them in the area near the lever. However with stimulus-bound gnawers the interaction with the wood may form a response chain that allows continuous engagement in the task thereby facilitating the reinitiation of the bar press response.

The fact that the latency for the first bar press re-

sponse was shorter when goal objects were present suggests that most of the differential bar press rates may be due to the differential latencies. However, this was not the case. The average latency for the first response to occur was only 20 seconds longer when the goal objects were available. If an animal were to perform at maximum efficiency during the 20 second interval the maximum number of 3 second reinforcements would be fewer than seven. However the obtained data indicate that 26.6 more stimulations per trial were delivered when the goal objects were present. This is of critical importance owing to the fact that Mendelson (1967) has suggested that the incentive qualities generated by the presence of the goal object induce the animal to press the bar. The present data show that less than one-third of the differential reinforcement rate could be accounted for by the visual or olfactory incentive qualities of the goal object. Furthermore, the fact that all animals were water satiated at the beginning of the session and then drank 10 - 15 cc of water during the 32 minute test session makes an interpretation based on the incentive qualities of the water doubtful. Thus it is more accurate and consistent with the present data to suggest that the major source of reinforcement arises from the physical interaction of the animal and the goal object. This is not to deny the fact that incentive qualities may be present, but rather to em-

phasize the importance of the consummatory response in maintaining stimulus-bound behavior.

A second important finding showed that the stimulation current itensity threshold for all three classes of stimulus-bound behavior was lower than the self-stimulation threshold. Also the self-stimulation threshold was generally lower than the current used to initially elicit stimulus-bound behavior during screening. The finding that intensities needed to produce self-stimulation are greater than the stimulus-bound thresholds supports and extends the earlier report by Coons and Cruce (1968). However, the fact that screening intensities exceeded the self-stimulation threshold has important implications concerning the role that ESLH may play in positively reinforcing or shaping stimulus-bound behavior early in screening.

GENERAL DISCUSSION

Stimulus-bound behavior has been shown to be flexible or plastic (Valenstein, Cox and Kakolewski, 1969). Other research has supported the position that the ESLH (Hoebel and Teitelbaum, 1962; Mendelson, 1967) and the response (Valenstein, Cox and Kakolewski, 1970) is reinforcing in stimulus-bound animals. Based on these results this dissertation attempted to combine the ESLH with a specific response so that the type of stimulus-bound behavior to subsequently emerge could be controlled. The results indicated that a contiguous relationship between the ESLH and a drinking response was not sufficient to affect the type of stimulus-bound behavior that emerges.

A second set of experiments was designed to determine the sources of reinforcement that play a role in maintaining stimulus-bound behavior once it has occurred. Specifically, animals were tested in a two-way shuttle situation so that the affective nature of the ESLH used in stimulus-bound studies could be assessed. The results showed that (a) animals given a choice between 30 seconds of unsignaled, non-self regulated ESLH and no ESLH had no clear preference; (b) animals that could control the frequency and duration of ESLH had no clear preferences when run at current intensities close to the stimulus-bound threshold, but showed a

slight preference for the ESLH at higher intensities that also produced consistent stimulus-bound behavior; (c) most animals showed a strong preference for the ESLH at all supra threshold current intensities when it was accompanied by a CS (light onset or light offset) and when they could regulate the delivery of the stimulation. These results generally supported the notion that the ESLH is a source of positive reinforcement in stimulus-bound animals.

Finally, animals were tested to determine if the performance of a consummatory response could be a contributing source of reinforcement in the stimulus-bound situation. Stimulus-bound gnawers as well as drinkers and eaters were found to bar press for ESLH at a higher rate when the appropriate goal object was present than when no goal objects were available. The relatively small difference in the latency to the first response on each trial as a function of goal object availability suggested that the performance of the response rather than the incentive qualities of the goal objects was responsible for the large differential bar press rate.

The earlier findings of Chisholm and Trowill (1971) offer evidence that the palatability of the goal object plays an important role in stimulus-bound drinking as well

as normal drinking. The data presented here concerning the rewarding properties of ESLH warn against making any basic assumptions concerning the uniformly positive valence of the stimulation in all stimulus-bound animals. The fact that non-self regulated ESLH delivered at long 30 second durations decreases the positive reinforcing effects of the stimulation suggests that the specific parameters utilized in a stimulus-bound study must be examined before any accurate statement concerning the affective nature of the stimulation may be made. An excellent example of the importance of parameters is available in a study by Phillips et al. (1969). In that study, 86 percent (19 out of 22) of the animals that were allowed to regulate the rate and duration of ESLH became stimulus-bound object carriers. Furthermore the average stimulation duration when objects were present was only 2.9 seconds. Comparing the 86 percent success rate of Phillips et al. with the usual 30 percent stimulus-bound success rate shows the effect of maximizing the positve reinforcement value of the ESLH.

Valenstein's interpretation (Valenstein, Cox and Kakolewski, 1970) which deemphasizes the rewarding qualities of ESLH in favor of the reinforcement arising from the performance of the consummatory response is not

accurate for two reasons. First, tests which evaluate the strength of reinforcement stemming from the ESLH or the performance of the consummatory response have been run in independent experimental settings. A test of the strength of the two sources of reinforcement relative to one another has not been made. Second, some reference must be made concerning the parameters of the ESLH due to the fact that the reinforcing value of ESLH changes as a function of the duration and the ability of the animal to regulate the delivery of the stimulation.

One important question left unanswered is why the initial stimulus-bound response to emerge cannot be manipulated by previous experience with a goal object in the presence of ESLH. If the sources of reinforcement have been accurately identified then it should be possible to combine them such that the initial stimulus-bound behavior is affected. Several possible reasons for the failures to manipulate the type of stimulus-bound behavior to initially emerge are apparent. First, it is possible that the temporal relationship between the response and the ESLH has not been optimal. Rather than having the consummatory response precede stimulation onset perhaps it would be beneficial to have it precede the offset. Second, it is possible that the various sources of reinforcement

do not have meaning until they are combined in the stimulus-bound situation. That is, the consummatory response, the ESLH and the incentive qualities of the goal object may all have to occur simultaneously in order to affect behavior. The individual manipulations of the consummatory response (Cox et al., 1970) or the lack of contiguity between the various components may decrease the effectiveness of the reinforcers to such an extent that behavior is not affected.

In summary, this research has demonstrated that reinforcement arising from the incentive qualities of the goal object, the ESLH, and the performance of the consummatory response all contribute to the maintenance of stimulus-bound behavior. It was also shown that stimulus-bound behavior was maintained better when several of the sources of reinforcement were present.

Implicit in the present results is the fact that future research should investigate more closely the role of ESLH as a source of reinforcement in stimulus-bound behavior. Attempts should be made to maximize the strength of the rewarding ESLH by using short durations of stimulation and by allowing the animal to regulate the rate at which the stimulation is delivered. With this procedure it should be possible to increase the percentage of stimulus-bound animals so that nearly all of the animals which

bar press for ESLH will also exhibit some type of stimulus-bound behavior. If we can demonstrate that stimulus-bound behavior is under the control of reinforcement arising from ESLH then the phenomenon will lose many of its mystical aspects.

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LIST OF APPENDIXES

APPENDIX A

Mean Sucrose lick rate per minute during testing for Experiment 1

Subject No.	Electrical Stimulation	Days 1	2	3	4	5
13	off	126	188	102	136	180
	on	110	144	80	122	168
28	off	170	212	22	-*	-
	on	192	204	30	-	-
29	off	130	72	50	54	152
	on	98	64	46	36	130
30	off	90	134	52	106	74
	on	42	76	64	68	58
31	off	82	176	100	116	114
	on	92	200	148	154	156
33	off	128	-*	76	104	112
	on	86	-	56	88	112
34	off	2	-	20	6	46
	on	202	-	250	332	268
35	off	182	-	102	186	216
	on	146	-	104	148	162
36	off	64	-	72	98	112
	on	80	-	52	82	98
37	off	216	-	124	166	162
	on	230	-	74	126	132

* Due to equipment failure data is not available for these cells.

APPENDIX B

Number of minutes on the unsignaled ESB side of the shuttle box during 24 minute sessions for animals run at medium current intensity.

Subject No.	Days 1	2	3	4	5	6	7	8	9	10
1	12.5	15.5	14.4	15.4	15.7	11.2	14.2	14.8	16.0	16.5
2	15.6	17.7	17.2	17.9	18.0	7.9	11.7	15.1	9.2	13.0
3	11.7	15.0	16.0	16.3	15.2	12.4	14.9	11.1	15.3	14.8
4	16.7	16.0	15.8	16.1	15.9	7.9	10.6	12.1	12.6	14.7

APPENDIX B

Mean time in minutes spent on the ESB side of the shuttle box during 24 minute sessions. Subjects could control the frequency and duration of the stimulation and were run at low current intensity.

Subject No.	Average Stimulation Duration*	Days					
		1	2	3	1	2	3
1	20.5	21.1	16.6	21.8	15.6	2.3	2.7
2	21.4	10.9	9.7	12.2	7.8	9.5	5.0
3	9.5	9.2	5.7	7.5	5.4	5.4	6.6
4	20.3	12.5	20.6	18.0	10.5	8.0	11.1

*Seconds.

APPENDIX B

Mean time in minutes spent on the signaled-ESB side of the shuttle box when the subject could control the frequency and duration of the stimulation. These subjects were run at low current intensity.

Subject No.	Average Stimulation Duration*	Days					
		1	2	3	1	2	3
1	24.1	19.1	20.9	22.9	21.8	23.1	23.0
2	25.5	15.0	18.1	22.1	17.5	21.7	22.1
3	13.7	12.7	9.3	9.5	5.8	15.3	7.8
4	24.5	21.0	22.1	20.1	21.2	22.9	22.9

APPENDIX C

Total bar presses per rat per day as a function of goal object availability

Subject No.	Day	Goal Object Available	Goal Object Not available
31G	1	117	17
	2	101	36
	3	93	5
	4	186	73
47D	1	91	55
	2	66	37
	3	88	69
	4	105	48
53D	1	104	21
	2	135	37
	3	129	27
	4	159	39
76G	1	56	15
	2	76	21
	3	65	54
	4	110	83
77E	1	53	14
	2	41	40
	3	76	49
	4	71	32
79D	1	95	3
	2	72	8
	3	150	17
	4	124	17

Note: G = gnaw, D = drink, E = eat

APPENDIX C

Water intake in cc for the last two days of testing

Subject No.	Day	Left Side	Right Side	Total
47D	3 4	4 6	3 1	7 7
53D	3 4	13 14	3 2	16 16
79D	3 4	3 3.5	7 7	10 10.5

APPENDIX C

Mean latency in seconds to the first bar press on each trial for the last two days of testing

Subject No.	Day	Goal Object Available	Goal Object Not Available
31G	3	67.6	97.1
	4	56.2	66.3
47D	3	12.3	15.8
	4	4.3	21.7
53D	3	37.8	71.5
	4	15.7	49.5
76G	3	6.1	3.2
	4	1.9	2.1
77E	3	9.3	8.6
	4	4.2	13.7
79D	3	28.0	95.0
	4	28.0	60.0

APPENDIX C

Total number of electrical brain stimulations per rat per day as a function of goal object availability

Subject No.	Day	Goal Object Available	Goal Object Not Available
31G	1	98	17
	2	60	25
	3	61	8
	4	105	66
47D	1	88	55
	2	61	30
	3	80	64
	4	97	45
53D	1	99	20
	2	131	34
	3	117	23
	4	137	35
76G	1	56	15
	2	76	21
	3	65	54
	4	109	83
77E	1	52	14
	2	38	35
	3	74	49
	4	70	32
79D	1	75	2
	2	62	6
	3	121	12
	4	109	15