THE ESTABLISHMENT OF DURABLE RESISTANCE TO EXTINCTION USING STIMULI PREVIOUSLY PAIRED WITH LATERAL HYPOTHALAMIC INTRACRANIAL STIMULATION

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ABSTRACT

Two experiments were concerned with the establishment of durable resistance to extinction using stimuli previously paired with the opportunity to obtain lateral hypothalamic brain stimulation. In the first experiment both a discriminative stimulus and a classically-conditioned stimulus were presented. In the second experiment the discriminative stimulus was omitted. In a two-lever Skinner box, the operation of a permanent lever introduced a retractable lever on which the subcortical stimulation was available. The two peripheral stimuli were associated with the insertion of the bar on which the brain stimulation was available. Two response measures were recorded on the permanent lever. The first measure was the number of bar presses. The second measure was the percentage of these presses which occurred within a 15 second interval after the presentation of the discriminative stimulus. The results of the two experiments were consistent with the view that positive lateral hypothalamic brain stimulation acts in a manner similar to peripheral primary rewards. More specifically, it was demonstrated that a discriminative stimulus (and possibly an accompanying classically-conditioned stimulus) can operate to produce resistance to extinction, when the response is antecedent to the act delivering the brain stimulation. It is suggested that this increased resistance to extinction

is possible only when the delay of reinforcement and the response topography is similar to that used to establish resistance to extinction with peripheral reward.

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In the fifteen years that have elapsed since Olds and Milner (1954) presented data which suggested a physiological basis of reward, controversy has raged concerning whether the behaviour elicited by intracranial brain stimulation (ICS) indeed reflects operation of normal reward mechanisms. Olds and Milner found areas in the septal and hypothalamic regions of the brain where a rat would stimulate itself frequently and regularly for long periods of time if permitted to do so. This repetition of an activity (e.g., bar-pressing) which preceded the ICS was thought at the time to be subject to the same laws as conventionally-reinforced behaviour. Subsequent investigation has found that the characteristics of behaviour rewarded by ICS correspond in some respects with those of behaviour rewarded in a normal, peripheral manner (e.g., food), but some striking differences have been encountered.

Before entering into a discussion concerning the differences between ICS and peripheral reward, some mention should be made regarding the various species in which rewarding brain stimulation has been found, and the areas of the brain responsible for the effect. Although the majority of the studies published and discussed later in this paper involve the rat, a number of researchers have utilized cats and monkeys. Roberts (1958) reported rewarding effects of posterior hypothalamic stimulation in the cat, and two studies (Schnitzer, Reid & Porter, 1965; Wilkinson & Peele, 1963) report training cats to bar-press for stimulation of the lateral hypothalamus and the medial forebrain bundle region. Work with monkeys has shown their capability to press a lever to obtain ICS on both limited VI and FR schedules, depending on the electrode placement (Brady, 1961; Brodie, Moreno, Malis & Boren, 1960; Porter, Conrad & Brady, 1958). Four other mammals with which the ICS effect has been demonstrated are the dog, rabbit, gerbil, and dolphin. Stark and Boyd (1961) reported that dogs will bar-press at a sustained high rate for electrical stimulation of the posterior hypothalamus, as will also the gerbil (Kramis & Routtenberg, 1969). Rabbits have been trained to push a chin lever to gain electrical stimulation of the septal area (Campbell, 1968). One of the most intriguing mammalian species in which reward centers have been found is the bottlenose dolphin (Lilly & Miller, 1962). These aquatic mammals learned not only to push a rod but also to vocalize for stimulation of the caudate nucleus. Three non-mammalian species have also received some attention. Macphail (1968) found that electrical stimulation of the forebrain of pigeons had reinforcing properites, although it was noted that they did not work for the ICS in the absence of prior food-rewarded sessions. Chicks, in contrast to pigeons, apparently need no prior experience with a peripheral reward. Andrew (1967) reported that chicks peck at a high rate, giving, in association with self-stimulation, vocalizations of a type given to a variety of sources of stimulation which chicks tend to approach (food, imprinting object, etc.). The lowest species, phylogenetically speaking, that has demonstrated positive intracranial reinforcement is a teleost - the goldfish. Boyd and Gardner (1962) trained goldfish to shuttle in a tank position task in which the positive side was reversed between trials. In addition to the shuttling task, the fish learned to strike a target to receive ICS when a cue light was present, giving evidence of discrimination.

In the studies mentioned above, it can only be inferred that the brain stimulation was "rewarding". A small number of clinical studies using human neuropsychiatric patients, however, gives us some direct, although possibly unreliable, information regarding the experiential effect of ICS. Patients equipped with portable self-stimulators have stimulated their own brains by means of a button switch wired into the circuit, and in association with the ICS have expressed feelings of comfort, relaxation, and joy (Heath, Leach & Byers, 1963; Sem-Jacobsen, 1959). Other effects of ICS reported are increased alertness, more rapid speech, and the expressed desire for repeated stimulation (Heath & Mickle, 1960). One attempt has been made to investigate human ICS behaviour approaching strict laboratory conditions characteristically used in animal studies (Bishop, Elder & Heath, 1963, 1964). Brain areas found to yield rewarding stimulation in the patients were the caudate nucleus, the septum, and the posterior hypothalamus. Each of two patients was equipped with a lever and hand button by which he could stimulate his own brain. Using three methods, termed "three current levels", "free choice", and "forced choice", the two patients showed reliable behaviorial evidence of the reinforcing effects. It was reported that the patients disregarded attractive food when permitted to self-stimulate, even when they had been food-deprived for seven hours.

The studies cited above implicate the lateral and posterior hypothalamus, the medial forebrain bundle, the septal area, and the caudate nucleus in the reinforcing effect, dependent on the species. The anatomical localization of reinforcement effects has been examined thoroughly in the rat. Olds and Olds (1963) found that only the lateral hypothalamus and the medial forebrain bundle yield pure positive reinforcement, while the septal and medial hypothalamic areas yield mixed positive and negative (aversive) effects. Other differences between medial forebrain bundle - hypothalamic placements and those of the septum have been reported (Olds, Travis, & Schwing, 1960). The rate of bar-pressing is greater with the former sites. In addition, hypothalamic stimulation seems to produce heightened general activity (Roberts, 1958) while septal stimulation appears to inhibit general activity, arresting running performance in a maze for long periods (Olds, 1956). Hypothalamic self-stimulation, in contrast to septal self-stimulation, seems to be resistant to decrements in response rates. In 48-hour tests, rats with hypothalamic electrodes self-stimulated to exhaustion and howed no decrement in response rates. Rats with septal placements, however, showed slowing of self-stimulation after four to eight hours of continuous responding.

These differences between hypothalamic and septal positive reinforcement are of considerable importance in the analysis of relationships between secondary reinforcement and ICS reward. Our examination of differences between the characteristics of behavior rewarded with normal peripheral rewards and those of behavior rewarded with ICS center around reports of discrimination learning, runway and T-maze performance, the effect of lengthening intertrial intervals, ease of establishment of intermittent schedules, and the phenomena of extinction and secondary reinforcement. Some of the differences between the characteristics of these two types of reward may be resolved if the nature of the reward is taken into account, i.e., if the procedure using ICS is modified to allow for an antecendent operant response to occur. The research presented later in this paper centers around such procedural modifications in an attempt to infer secondary reinforcement through the demonstration of resistance to extinction.

The original study of the effect of ICS on discrimination learning found an inhibitory effect of reinforcing septal and hypothalamic ICS on rat discrimination learning using water as the operant reinforcer (Stein & Hearst, 1958). Subsequent research indicates this finding is restricted to the case of ICS presentation superimposed on discriminative responding for a peripheral reward, and does not pertain to situations where discrimination learning is reinforced with brain stimulation to the posterior and lateral hypothalamic placements (Beer and Valenstien, 1960; Keesey, 1964b; Keesey, 1966; Kling & Matsumiya, 1962). Beer and Valenstein showed that rats were capable of discriminating between two auditory stimuli (A and B) during intracranial stimulation when responses on a second bar were rewarded with food only during tone A periods. Results showed that rats reliably switched to the food lever only during the tone A periods, and immediately returned when tone A ceased. Using a more conventional paradigm, Keesey (1964b) trained rats to make a brightness discrimination, and reported that the rate of learning was a decreasing function of the delay of reward, indicating a lack of inhibitory effect of ICS. A similar, subsequent study by the same researcher (Keesey, 1966), in which current and frequency parameters of the ICS were varied, indicated that the effects of the ICS on the rate of discrimination learning are independent of the motivating properties of that same stimulation. Current level did not influence the rate at which the discrimination was acquired, in spite of the fact that it affected different response rates. Kling and Matsumiya (1962) made direct comparisons of the relative permanence of discriminations rewarded with food and with ICS, and reported that discriminations rewarded with the ICS were at least as permanent as those rewarded with food. The authors, training rats in a visual brightness discrimination-reversal task, found that animals trained with either food or ICS were not different on the first-task performance, but that reversal training was slower if the first discrimination had been learned with ICS. Further evidence suggesting that the discriminability of sensory stimuli may not be influenced by the type of reinforcement used during training has been presented by Terman and Kling (1968). Following an initial procedure similar to that of Keesey (1964b), the luminance difference of the discriminative stimulus was then reduced in discrete steps for both food and posterior hypothalamic-ICS groups. Even with this increased difficulty of discrimination, no differences were found between the two types of reinforcement. In addition to these findings, stimulus generalization gradients for septal ICS, posterior hypothalamic ICS, and food reinforcement have been reported to be similar (Kling & Berkley, 1968). Kling and Berkley trained rats to make an auditory discrimination, and then tested for stimulus generalization. Typical acquisition and generalization curves were obtained from all groups, the generalization curves being obtained in both reinforcement and extinction tests. These last findings strengthen the previous conclusions that sensory discrimination control of ICS-maintained behavior can in fact be produced in a number of differing situations, suggesting that at least in this respect ICS - rewarded behavior is similar to that rewarded peripherally.

In contrast with studies involving merely a sensory discrimination, runway and maze performance rewarded by ICS differs considerably from its peripherally-rewarded counterpart. The first study of runway and maze behavior controlled by ICS was that of Olds (1956), in which baso-medial-forebrain ICS was compared to food reinforcement. It was reported that both reward groups showed improvement in the runway and the maze (Lashly III Type), but only when run under 24 hours food deprivation. In the runway, the ICS produced a better average performance than did the food, while in the maze the central reward produced slower learning and more errors than the peripheral reward, but approximately the same speed of performance after 45 trials. The most important finding, however, was that the ICS-rewarded behavior, in comparison to food reward, showed a strong overnight decrement with a large "warming-up" phenomenon the following day, indicating that massing of trials may be necessary to maintain performance with ICS-rewarded runway and maze behavior.

The importance of massed trials for ICS-rewarded runway performance has been verified by Seward, Uyeda, and Olds, (1960), who trained non-deprived rats, using hypothalamic ICS, 10 trials per day for 12 sessions, to run in a straight runway. It was found that the rats ran almost twice as fast after 12 days of training if the trials were separated by 20-second intertrial intervals, rather than if they were spaced by 15 minutes. Both "passive" and "active" methods of ICS administration showed this difference. These findings are supported by those of Spear (1962), who reported that massed training with septal ICS resulted in increasing runway speeds both within days and between days, while a spaced group decreased in speed within and between days. The between-trial or overnight response decrement typically found in the studies using ICS reward contrasts with the situation normally encountered with food reinforcement. This response decrement encountered with ICS reward may be alleviated, however, by first providing the subject with trains of ICS noncontingent on the runway or maze response ("priming"). Wetzel (1963) has reported that 2.5 minutes of self-stimulation prior to trials spaced one day apart enables rats to improve performance in a runway.

Gallistel (1966, 1967) has systematically examined the effect of varying the intertrial interval. The speed of traversing a runway for septal or lateral hypothalamic ICS was found to be inversely related to the interval between successive trials. In contrast to a water-reinforced group, increasing the intertrial interval from 5 to 60 seconds decreased the running speed, and decreasing the interval from 60 to 5 seconds increased the running speed. This change of running speed occurred immediately on the first post-shift trial, suggesting the presence of a rapidly-decaying motivation. The possibility of drive-decay is further supported by the fact that when subjects were run in strict alternation in two runways (black vs. white) for unequal ICS, they ran faster to the lower ICS even though, when allowed to choose, they showed no such preference. At present some controversy exists on whether this "contrast effect" can be best accounted for by a "drive-decay" or "incentive change" explanation, the differences in interpretation being subtle and possibly existing only on a terminological level (Gallistel, 1969 ; Panksepp, Gandelman & Trowill, 1968, 1969).

In contrast to the above studies of runway and maze performance, a few studies using ICS reward report results similar to those using peripheral rewards (Kornblith & Olds, 1968; Scott, 1967). Scott encountered no problem training lateral-hypothalamic and medial-forebrain bundle rats in a straight runway with spaced trials, but did find some difficulty with septal placements. The hypothalamic ICS group demonstrated both that "priming" was unnecessary and that a "warm-up" period was not required. Kornblith and Olds extended Scott's findings and successfully trained rats with lateral hypothalamic ICS on position-discrimination reversal problems, even though the trials were separated by 24 hours.

The placement of the electrode may be critical in these studies, however, as Bull (1968) failed to show any learning whatsoever in a T-maze situation over 5 days of 10 massed trials per day. Bull, in variance with other researchers, used posterior hypothalamic ICS, which may account for his negative findings. A final study which presents an interesting but perplexing finding is that of Wasden, Reid, and Porter (1965). Wasden et al. reported finding the classical overnight decrement in runway performance demonstrated by a number of the studies, but found that this decrement could be alleviated by making the first trial of the day an extinction trial!

In comparison to the literature on ICS-maintained discrimination learning, studies of ICS-maintained runway and maze performance show some prominant differences between centrally and peripherally-rewarded responses. Deutsch and Deutsch (1966) and Gallistel (1964) suggest that a rapid decay of the motivating effect of ICS (independent of its reinforcing effect) may account for the beneficial effect of "priming" and the massing of trials on runway and maze performance. The "drive-decay" theory assumes that the ICS excites two types of pathways between groups of cells - reinforcement pathways and motivational pathways. It is hypothesized that ICS therefore provides the "reward" for the last response, plus the "motivation" for the next response. This artificially-induced motivation is thought to decay rapidly to its pre-stimulation level, which is determined by the normal drive present in that specific motivational pathway. "Priming" or massing of trials is thought to provide motivation for subsequent performance of the reinforced response. The same authors propose that the same theory may account for several phenomena yet to be discussed - rapid extinction, difficulty in establishing secondary reinforcement, and poor performance on intermittent schedules when compared to peripheral reinforcers. In the light of the close parallel between the characteristics of central and peripheral reward on discrimination learning, and the evidence that with some placement-procedural combinations normal runway and maze performance can be maintained by ICS, the generality of the "drive-decay" theory is questionable. Adding to the inadequacy of this theory is the finding that discrepancies between central and peripheral reward pertaining to secondary reinforcement, intermittent schedules, and resistance to extinction appear to be vastly diminished when procedural allowances are made for the central-peripheral difference in reward stimulation, i.e., the lack of an antecedent response in the typical ICS paradigm.

Although there have been reports of secondary reinforcement using septal ICS as the primary reinforcer, attempts to obtain secondary reinforcement using hypothalamic stimulation as the primary reinforcer have been unsuccessful. Stein (1958), using septal implants, demonstrated secondary reinforcement with a classical conditioning paradigm. The operant lever-pressing rate was obtained for each rat in the presence of two bars, the operation of one which led to a tone. After this initial testing, 400 pairings of the tone and septal ICS were administered with the levers removed. The levers were then replaced once again and the rate of bar-pressing was obtained for each individual rat. Results showed that there was a significant increase in the rate of pressing of the bar that produced the tone. More recently, Knott and Clayton (1966) have confirmed the findings of Stein, but again using septal placements. Knott and Clayton paired tone and ICS intermittently for one group and continuously for another, with a third (control) group receiving no ICS. It was found that both experimental groups showed significant preference for the lever which led to the tone, but that the effect was greater for the partial paired group, for which ICS followed the tone 50% of the time.

In contrast to the studies using septal implants, the two studies utilizing hypothalamic electrodes failed to demonstrate secondary reinforcement. Seward, Uyeda and Olds (1959) compared two methods - a discriminative procedure in which light signalled the occurrence of ICS, and a classical conditioning procedure in which light occurred simultaneously with the ICS. Results indicated that a neutral stimulus associated with hypothalamic ICS significantly increases the post-training operant bar-pressing level compared to the pre-training level. There was no significant difference between the discriminative and classical conditioned groups, and although the results suggest the establishment of incentives, there was no demonstration of differentially-conditioned stimuli. The second study using hypothalamic placements was conducted by Mogenson (1965). Using a paradigm similar to Stein (1958), Mogenson was unable to replicate the findings of the former author. He suggests that this failure is attributable to disruptive effects of the ICS which interfore with the associative linking of it with the contiguously occurring buzzer or light.

In addition to the failure to demonstrate secondary reinforcement with hypothalamic ICS, the literature indicates that, using conventional training paradigms, it is difficult to maintain intermittent reinforcement schedules in the range of parameters ordinarily used with food as a reinforcer. Sidman, Brady, Boren, Conrad, and Schulman (1955) found that rats will not learn to press a bar for ICS on schedules beyond FR 7 or VI 16 seconds, whereas with food reinforcement FR 100 and VI 5-minute schedules maintain performance (Ferster & Skinner, 1957; Jenkins & Stanley, 1950). It was reported that the rats pressed for a short while after the hypothalamic ICS had been turned off, but not a sufficient number of times to bridge the gap. Elder, May and Rye (1965) report that for FI 60 second to FI 120 second schedules the overall rate of bar-pressing for medial-forebrain bundle rats is less pronounced than that characteristic of food-controlled FI schedules. These authors also found it necessary to "prime" and "retain" rats at the beginning of each session, even when they had been previously exposed to the schedule for as many as 28 hours.

The question arises as to why secondary reinforcement has not been demonstrated with hypothalamic implants, and whether this may be related to the nature of hypothalamic ICS as a primary reinforcer. One reason may be that many previous experiments have not utilized paradigms which are analogous to those used to establish behavior supported by partial peripheral reinforcement. Why this may be critical for hypothalamic implants but not for septal sites is not immediately clear. However, it is of importance to note in past experiments where ICS served as the "reward", the "reward" was delivered upon bar-pressing. In this situation, the animal does not have to learn a conditioned relation between two situations as in the case of instrumental responding for food. In other words, the situation is less like an instrumental response and more like a consummatory response, e.g., drinking, when each swallowing response delivers the reward. The studies of Egger and Miller (1962, 1963) suggest that this state of affairs may make the establishment of a secondary reinforcer difficult, as the stimulus paired with the ICS has little informational value. The study of Schoenfeld, Antonitis, and Bersh (1950) supports this suggestion. A one-second light was presented while the rat was eating, rather than just before food delivery as is the usual method. The authors were unable to demonstrate that the light was a conditioned reinforcer during extinction trials, using this unusual method.

Recent studies do, however, indicate that adequate performances can be obtained using intermittent hypothalamic ICS in the range of parameters ordinarily used with food as a reinforcer. The same studies suggest the possibility that hypothalamic ICS may affect behaviour precisely as other rewards do (including the establishment of secondary reinforcement), provided the delay of reinforcement and nature of response are equated. Two investigations (Hawkins & Pliskoff, 1964; Pliskoff, Wright & Hawkins, 1965) demonstrate that FI, FR, DRL and VI schedules can be maintained with hypothalamic ICS if the lever press is in the same relation to the ICS as the complex consummatory response bears to the ingestion of food. These experimenters trained rats to press a permanently mounted lever in order to produce, on a schedule, (eg. VI 30 seconds) a second, retractable lever. The ICS was programmed on this retractable lever. Following completion of a programmed number of CFR response stimulations (eg., 5), the bar retracted from the box. Thus the pressing for the ICS is clearly the consummatory response whereas responding to the first bar corresponds to the bar-press ordinarily antecedent to consumption of food. Although these authors did not attempt to demonstrate secondary reinforcement using a specific stimulus, the paradigm does provide for conditioned reinforcement and this may account for the sustained performances on the intermittent schedules. Gibson, Reid, Sokai, and Porter (1965) have suggested that the nature of the response is of primary importance, rather than the type of reinforcement, in establishment of secondary reinforcement. Rats were trained in an operant situation, with two variations of the common reward procedure. One group of rats was required to press the bar for water, while the other pressed for ICS. These two groups were further split into subgroups, one which received reward on an immediate reinforcement schedule, and the other which received its delayed reward at a dipper cup some distance from the lever. Resistance to extinction was greater for the rats that received ICS reward distant from the lever - the resistance to extinction equal to that of rats rewarded with food. The results of this study, however, could be explained by the delay of reward rather than distance per se.

A second possible factor contributing to past failures to demonstrate secondary reinforcement (and sustained performance on intermittent schedules) using hypothalamic ICS as the primary reinforcer may be the inadequate primary reinforcer used during secondary reward training. It has been demonstrated with normal reinforcers such as food, using within-subject designs, that the strength of a secondary reinforcing stimulus varies directly with the amount of primary reinforcement used during training (Butter & Thomas, 1958; Stebbins, 1959). It would seem that one cannot predict ICS-reward values solely on the basis of the rate of responding. Recent studies show that rats, when given a preference, choose hypothalamic current intensities at higher levels than those intensities eliciting maximum bar-pressing rates (Hodos & Valenstein, 1962; Valenstein, 1964). The schedule also may be of importance when considering reward values. Sidman et al. (1955) reported that FR schedules were extremely sensitive to small changes in intensity of ICS. Herberg (1963) reports that sustained responding on partial reinforcement cannot be obtained with near-threshold currents. McIntire and Wright (1965) replicated Keesey's (1964a) earlier observations which suggest that optimal stimulus durations increase on aperiodic (eg., FR 5) schedules of reinforcement. Using the apparatus mentioned previously, Hawkins and Pliskoff (1964) found that the rate on a permanent VI lever continued to increase beyond the intensity value which produced peak rate on the retractable ICS lever. It thus becomes clear that ICS reinforcement strength cannot be assessed adequately by self-stimulation rate. The microcoulombs (Keesey, 1962; McIntire & Wright, 1965) yielding maximum hypothalamic reward value may in fact yield decreased ICS bar-pressing because of changes in activity level and performance capabilities (Valenstein &

Meyers, 1964).

A third factor which may have hindered the demonstration of secondary reinforcement in the past is the lack of an adequate relevant "drive intensity" at the time of the test. Miles (1956) reports that the strength of secondary reinforcement varies directly with the drive intensity at the time of testing. For example, effects of lateral hypothalamic ICS appear to be selectively affected by variations in the degree of food deprivation. Hoebel and Teitelbaum (1962) report that hungry lateral hypothalamic rats self-stimulated more frequently than satiated ones. These authors also report that stimulation of the ventromedial nuclei (satiety center for hunger) reduced food intake and inhibited self-stimulation at sites in the lateral hypothalamus (feeding center). In addition, lesions in the area of the ventromedial nuclei increased food intake and lateral hypothalamic self-stimulation. It seems possible that the pleasure of lateral hypothalamic ICS may be similar to gratification obtained by eating. Support for this view comes from several sources. Sidman et al. (1955) found that the FR performances of rats with lateral hypothalamic implants improved under food deprivation. Similar results were obtained with bar-pressing by Olds (1958) and Wilkinson and Peele (1962). Margules and Olds (1962) found that all electrode sites from which feeding could be elicited by electrical stimulation also showed high rates of self-stimulation. The reward value of lateral hypothalamic ICS in relation to food reward is demonstrated by the fact that rats will "self-starve" themselves while responding for lateral ICS in the presence of food (Falk, 1961; Routtenberg, 1964; Routtenberg & Lindy, 1965; Spies, 1965). This self-starvation probably has a circular effect, the increased food deprivation leading to an enhanced ICS rate. Routtenberg and Lindy (1965) report that when the electrode cable became disconnected during the testing session, the self-starving rat would immediately cease bar-pressing for ICS and eat. It should be noted here that these effects are restricted to electrodes implanted in the lateral hypothalamus. One interpretation is that lateral hypothalamic ICS may momentarily but simultaneously activate neural feedback from consummatory food responses, the upper G.I. tract, and blood glucose level (Stellar, 1954). If this is in fact the case, hunger drive during the acquisition of secondary reinforcement using lateral hypothalamic ICS may be of some importance, and may be absolutely essential for the demonstration of the secondary reward during the subsequent testing.

The importance of hunger drive during extinction for lateral hypothalamic implants has been experimentally demonstrated. Deutsch and Howarth (1963) report that time to extinction is prolonged under food deprivation. Normal extinction curves are reported to occur only in hungry lateral hypothalamic rats (Olds, 1956). Deutsch and DiCara (Deutsch & Deutsch, 1966) found a high correlation between the number of presses during extinction and degree of hunger. These author used a within-subject design, alternating deprived and satiated conditions between two groups of rats, utilizing pairs of 3-minute extinction sessions. The same two authors (Deutsch & Deutsch, 1966) report a high correlation ($r = .89$) between the rate of responding for ICS measured during hunger, and the degree of secondary reinforcement found under the same drive condition.

Thus the previous evidence seems to suggest that the optimal conditions for the demonstration of secondary reinforcement include:

(a) A paradigm analagous to those used to establish behaviour supported by partial, peripheral, primary reinforcement.

(b) Stimuli with some informational value relative to the presence of primary reinforcement.

(c) Adequate primary reinforcement during the secondary reward training.

(d) Adequate drive intensity at the time of the test for secondary reinforcement.

In this experiment the test for secondary reinforcement was the degree to which resisteance to extinction was greater on sessions when stimuli previously paired with ICS were present, compared to sessions when such stimuli were absent. The paradigm used to demonstrate this resistance to extinction with hypothalamic implants is one which has the following general characteristics:

1. Within-subject design which allowed for individual rats, a comparison of resistance to extinction with and without the relevant stimuli.
2. A paradigm providing delay of reinforcement and response topography similar to that used to establish secondary reinforcement with peripheral primary reinforcement.
3. Adequate reward values of lateral hypothalamic ICS during training.
4. Maintenance of the relevant food drive throughout training and testing.
5. The use of two "secondary reinforcing" stimuli:
    - [i] a stimulus paired with primary reinforcement using a delayed classical conditioning procedure.
    - [ll] a stimulus signalling that primary reinforcement is now available, contingent on the subject's response.

Since past research using conventional reinforcers has demonstrated resistance to extinction using paradigms suggested by both the Discriminative and the Classical Conditioning hypotheses (Dinsmoor, 1950; Ratner, 1956; Wike, 1966), it was decided to incorporate both methods in this study, and by doing so to maximize the possibility of obtaining positive results.

Bersh (1951) and Jenkins (1950) have shown using normal primary reinforcers that the strength of secondary reinforcement decreases as the interval between the onset of the classically-conditioned stimulus and the onset of the primary reinforcement increases, the optimal interval being one second using either a delayed or trace procedure. It was decided to employ this interval in the study at hand. A stimulus paired with partial reinforcement in secondary reinforcement training tends to have greater secondary reward value than a stimulus paired with 100% primary reinforcement (Armus & Garlech, 1961). It would appear that intermittent presentation of primary reinforcement during training and intermittent presentation of secondary reinforcement during testing is the best method, and one which is utilized in the present study (Fox & King, 1961; Zimmerman, 1957). Because the reinforcing effectiveness of any stimulus is being extinguished while it is being studied, the intermittent presentation of primary reinforcement during training and the intermittent presentation of the conditioned reinforcer during extinction should slow the extinction process. Also, if the secondary reinforcer is presented according to a schedule, the pattern of responding that develops can be compared with the pattern that would be maintained by a schedule of primary reinforcement. Teichner (1952) has reported that resistance to extinction is greater when the intertrial interval used in extinction is the same as in acquisition. These findings with respect to the effect of reinforcement schedules were also utilized in the design of this experiment.

Given the previously outlined characteristics of the present experiment, it is hypothesized that the resistance to extinction of an operant response will be greater on those extinction sessions in which stimuli associated during training with accessibility to primary reinforcement (ICS) are present. It is predicted that the extinction of the operant response will occur across those sessions in which the stimuli are present as well as across those in which they are absent, but that in the former sessions the progressive decrement in responding will be more gradual. In other words, the effectiveness of the secondary reinforcers themselves can be expected to decline, although this rate of decline will be relatively low considering the training schedules used. In the case of the Discriminative stimulus, it is hypothesized that its presence during the extinction phase will produce, in addition to increased resistance to extinction per se, a temporal pattern of responding similar to that observed during training with the same stimulus on an identical schedule. The gradual disappearance of this patterning is predicted as the extinction trials with the Discriminative stimulus continue.

The first experiment combines the use of a Discriminative stimulus with a Classically-conditioned stimulus. The relative effectiveness of these two stimuli cannot be determined by increased resistance to extinction in their presence, but the effectiveness of the Discriminative stimulus (or at least the degree to which the subject utilizes its informational value) can be determined by observing the degree of temporal patterning of the responses.

The second experiment uses only a Classically-conditioned stimulus. Although increased resistance to extinction in its presence is hypothesized, in this second experiment no temporal patterning is predicted in either the training or extinction phases.

It is further hypothesized that extinction sessions with the stimuli present will produce significantly greater response measures than identical, initial operant level sessions, the difference the result of association of the stimuli with accessibility to ICS. Likewise, response measures obtained before this association should not vary significantly dependent upon the presence of the experimental stimuli.

Method

Subjects

The subjects were 12 male albino rats of the Sprague-Dawley strain, obtained from the Charles River Breeding Laboratories, Wilmington, Mass. At the time of the operation the rats were approximately 3 months old, and weighed between 300 and 325 grams. The rats were individually housed in stainless-steel maternity cages (9.5 inches long x 7 inches wide x 8 inches high), with sawdust bedding present in the enclosed bottom of the cages. Subjects were watered and fed ad. lib. until 2 weeks after the operation, at which time a 23 hour food-deprivation schedule was initiated.

Apparatus

During both the training and the testing, subjects were run in a two-lever Skinner box designed and constructed by the author (Figure 20, Appendix). The inside dimensions of the box were 11.25 inches long x 14.5 inches wide x 13 inches high. The front wall of the box was constructed of black plexiglass, with clear plexiglass constituting the sides (covered on the exterior with grey cardboard). The bottom of the box consisted of a grid constructed of steel rods, running parallel to the front panel. Situated on the front panel of the box, equidistant from both sides, were a small bulb and speaker, located at a height of 4 and 10 inches, respectively, from the bottom of the box. 75 db. white noise from a Grason Stadler white noise generator was delivered through the speaker, constituting one of two stimuli. The light, the second stimulus, consisted of a 1 1/4 inch diameter lamp programmed to provide a pulsating light of 2 cps. When this light was not pulsating, it provided an illumination of 20 foot-candles at a distance of 6 inches from the front panel. Both the auditory and the visual stimuli were selected for maximum attentional value. General illumination at the center of the Skinner box was supplied by a 60 watt bulb situated some distance from the apparatus. Projecting into the front panel, near the bottom and separated by 8 inches, were two levers -- one of which was retractable. The right bar was permanent and painted white. It was 1.75 inches in width and projected 2.25 inches into the box. The left lever was retractable and was constructed of brass 1.5 inches in width, and projected 1.25 inches into the box. The retractable bar could be inserted or withdrawn by a motor mechanism, the speed of insertion and withdrawal controlled by a rheostat.

Bar presses on the retractable bar resulted in 0.2 seconds of brain stimulation being delivered to the rat. An overhead mercury commutator with a vertical movement compensator (Berkley & Kling, 1967) handled the stimulation leads to the rat. The subcortical stimulation was provided by two

Grass model S4 stimulators. The output from the stimulators consisted of 100 cps. pulse pairs of biphasic square waves, separated by 0.2 msec. and 0.2 msec. in duration. The output from the stimulators was fed through a pair of Grass model SIU4678 stimulus isolation units, which insured isolation of the rat from ground. A 160K ohm resistor was placed in series with the rat, providing a relatively constant current. Current level and the voltage-drop across the rat were monitored simultaneously on a Tektronix model 502A dual beam oscilloscope. Grason Stadler programming equipment provided a maximum degree of automation to both the training and the testing of the subjects. The Skinner box was situated in a room well removed from the stimulating, programming, and recording equipment. Mechanical counters, a Gerbrands cumulative recorder, and a Rustrak four-channel recorder were utilized for the collection of the data.

Surgery

Under sodium nembutal anesthesia, a bipolar electrode (MS 303, Plastic Products Co., Roanoke, Virginia) was stereotactically implanted using coordinates designed to ensure placement in the MFB -- lateral hypothalamic area (DeGroot, 1959). The coordinates used were 5 mm. anterior of the O-Vertical-Plane, 1.8 mm. left of the Lateral-O-Plane, and 2.8 mm. below the Horizontal-O-Plane (DeGroot). Before insertion of the electrode, four small allen screws were threaded into holes drilled in the skull surface surrounding the electrode hole. After insertion of the electrode, acrylic cement was applied to the exposed skull, anchoring the electrode firmly to the four small screws and the skull (Figure 21, Appendix). After hardening of the cement, the open wound was lightly sutured. The animals were allowed to recover eighteen days before they were incorporated into the experiment proper.

Histology

Approximately one week after the last rat was tested, the 12 rats were sacrificed with sodium nembutal, and were then perfused with 9% saline solution followed by 10% formaldehyde. The skulls of the rats were placed in 10% formaldehyde, and the brains removed and placed in the same solution the following day. Several days later, the brains were frozen and sectioned. Photographs were taken of those 40μ sections which included the electrode tracts. These photographs were taken both before and after thionin staining.

Procedure

Subjects were assigned to Experiment I (8 rats) and Experiment II (4 rats) randomly before training commenced. The procedures followed with the two experiments will be treated separately. All rats were maintained under 23 hours food deprivation for the duration of the experiment. All sessions (operant, training, extinction) consisted of 30 minutes per day. Generally speaking, the designs of the two experiments take advantage of within - subject measures.

Experiment I. The 8 subjects of this experiment were randomly assigned to 2 groups (4 rats each). Group 1 differed from Group 2 in that with the former group the Discriminative Stimulus (S^D) was auditory and the Classically-Conditioned Stimulus (S^C) was visual. Group 2 had these modalities reversed.

Determination of operant levels (Days 1-4):

Before being treated with subcortical stimulation, all rats were tested for their operant level on the permanent bar (retractable bar withdrawn). The first two days of this phase of the procedure consisted of an absence of any experimental stimuli. The second two days consisted of the presentation of programmed stimuli identical to that encountered later during one of the extinction conditions. The details of the presentation of these stimuli will become clear later in the description of the extinction procedure. Briefly though, the first two days of operant level determination was identical to one extinction condition (no stimuli present), while the second two days of operant level determination was identical to the other extinction condition (stimuli present).

"Screening" and the initial training of subjects (Days 5&6):

All rats were tested for the positive-reinforcing properties of ICS on the inserted, retractable bar (the permanent bar removed). The minimum number of responses per 30 minute session required to determine whether to continue training was 300, using adequate current parameters. All twelve of the subjects met this criterion. Current parameters were further manipulated to produce a maximum sustained rate of bar pressing for the two days of this phase.

Training on the second bar - CRF & VI-15 sec. schedules (Days 7-11):

All subjects were now trained to press the permanent bar to gain access to the retractable (ICS) bar. The circuit was altered so that the retractable bar retracted out of the box after 5 stimulation-reinforced presses. A single response (after up to a 3 second delay) on the permanent bar then reintroduced the retractable (ICS) lever, with a one second latency, for another exposure to CRF-ICS-5. This schedule was maintained for three daily sessions, using those current parameters necessary for an optimal rate on the permanent bar. After three days on the CRF schedule, the presentation of the retractable lever was then moved to a VI-15 second schedule. This second schedule was maintained for two days, using current parameters necessary for an optimal rate on the permanent bar.

Secondary reward training:

On Day 12, the presentation of the retractable lever was moved to a VI-30 second schedule. Presses which were rewarded after one second by the introduction of the retractable (ICS) lever now resulted immediately in a 3 second stimulus (S^C). This may be considered a delayed conditioning paradigm. On Day 13, in addition to S^C, the termination of the VI-30 second period in which bar presses on the permanent bar resulted in no presentation of S^C or the retractable lever (and therefore the beginning of a period of potentially-rewarding responses) was marked by the onset of S^D, which terminated only after the subject made a subsequent response on the permanent bar. This training procedure was continued from Day 13 onward until two criteria were met:

1. The rate of bar pressing on the permanent lever stabilized to the extent that there was a change of less than 5% on three successive days.
2. 80% of the total bar presses on the permanent bar occurred 15 seconds after the onset of S^D, on each of the above three stabilization days.

The next schedule consisted of the VI-30 second schedule modified so that the presentation of the retractable (ICS) lever now occurred randomly on only 50% of the presentations of $S^D$and S^C, the latter two which remained on the VI-30 second schedule. The subjects were trained for one session per day until again they reached the two criteria used in the preceding schedule.

Test for resistance to extinction:

The day following the last VI-30 (50%) session, the rats were tested for resistance to extinction, with one session per day for ten days. Each individual rat underwent two different extinction conditions, the order of their presentation counterbalanced between rats. Two rats of each training Group (1 & 2) were subjected to one of the two orders of testing (four rats in all in each order of testing - two rats from Group 1 and two rats from Group 2, their designation randomly determined). The two extinction conditions were the following. In both conditions the retractable lever remained withdrawn.

[1] The same schedule as in the VI-30 second (50%) training, except that the retractable lever did not appear. This situation was identical to training except that here 100% (vs. 50% in training) of the permanent lever presses during S^D resulted only in S^C.

[2] S^D absent, with the responses on the premanent bar NOT leading to S^C. Again, as in the previous condition, the retractable lever was not present.

It should be noted here that the second extinction condition was identical to circumstances present during the first two days of operant level determination. The first extinction condition was identical to the situation present during the second two days of operant level determination.

The two orders of extinction testing were the following, the numerals representing the two extinction conditions.

	DAY 1	2	3	4	5	6	7	8	9	10
ORDERI	[1]	[2]	[1]	[2]	[1]	[2]	[1]	[2]	[1]	[2]
ORDER II	[2]	[1]	[2]	[1]	[2]	[1]	[2]	[1]	[2]	[1]

Experiment II. The four subjects of this experiment were randomly assigned to two groups (2 rats in each). Group 1 differed from Group 2 in that the former group was presented with the visual S^C. Group 2 was presented with the auditory S^C. Neither group in this experiment was presented with an S^D. The procedure in this experiment was identical to that of Experiment I, with the following exceptions:

1. No S^D was present.
2. For the VI-30 second and the VI-30 second (50%) schedules, only the first, stability, criterion was sought.
3. During extinction, each of the two testing orders contained one rat from each of Group 1 and 2, their designation randomly determined.

Dependent Response Measures

Two dependent measures were recorded on the permanent bar throughout the major portion of both experiments. The first measure, the number of bar presses on the permanent bar during a 30 minute session, was recorded on all days with the exception of during initial "screening" and training (Days 5 & 6). The second dependent measure was the percentage of presses on the former bar that occurred shortly (within 15 seconds) after each initiation of the Discriminative Stimulus (S^D). This post-S^D percentage was recorded under two conditions. In the first condition, the Discriminative Stimulus was actually presented to the rat. In the second condition, the Discriminative Stimulus was not presented to the rat, although programming equipment identified the interval (15 seconds) after the S^D would have been initiated. This allowed the percentage of permanent bar presses occurring 15 seconds after an actual S^D initiation to be compared with the percentage occurring within the same interval of the program, but in the absence of S^D initiation. This post-S^D percentage was recorded during the second two days of operant-level assessment, and during secondary reinforcement training and testing.

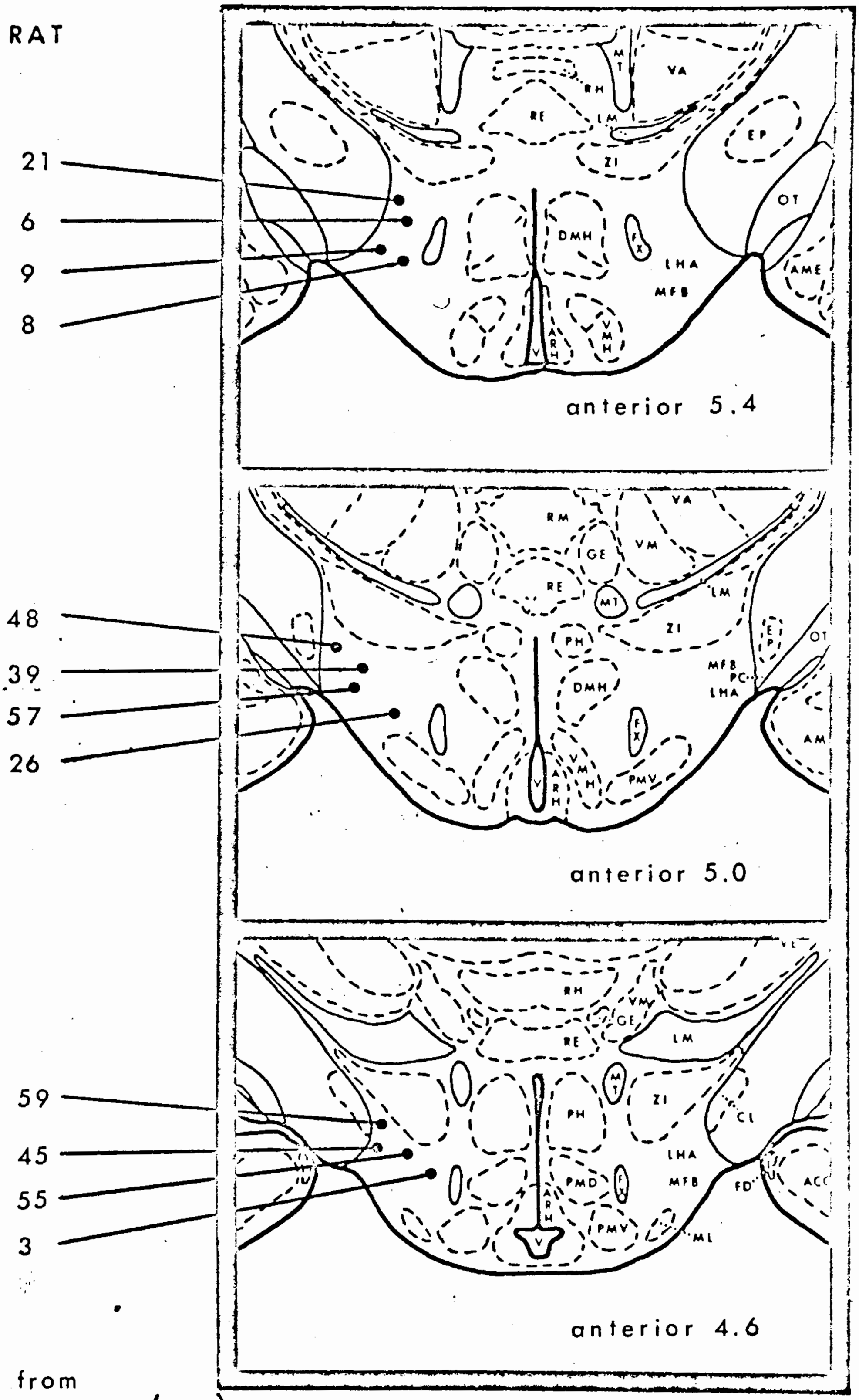
Results

The results of the histological analysis are presented in Figure 1. Examination of fresh, unstained sections showed all of the electrode tips to be in or directly adjacent to the lateral hypothalamus and medial forebrain bundle as drawn by Pellegrino and Cushman (1967). Photographs of both stained and unstained sections of the brains show specific points of electrode penetration. Figure 22 (Appendix) shows unstained sections for Rats 3, 6, 8, 9, 26, and 39. Figure 23 (Appendix) presents stained sections for all rats except Rat 3, the section of which was unavailable. Some difficulty was encountered in the fixing of the stained sections, this difficulty contributing to the poor quality of the photographic prints.

Table 1 shows the O-to-peak stimulating current used at the different stages of training in Experiments I and II. The lower limit of the current range was set by the finding that all rats failed to respond reliably during "screening" on current parameters below 0.4 milliamps. The upper limit of the current range (0.8 milliamps) was dictated by the capabilities of the stimulation and monitoring circuits. Within the above current range, increases in current intensity were inserted at two points -- one at the commencement of the second bar training, and the other on the second day of the

FIGURE 1 SUMMARY OF HISTOLOGY

Location of electrode tips



Brain sections from
Pellegrino and Cushman (1967)

TABLE I

SCHEDULE	BAR ON WHICH THE NUMBER OF RESPONSES WAS RECORDED							
	RECTRACTABLE (ICS) BAR		PERMANENT BAR					
	CONTINUOUS		CONTINUOUS			VI - 15 SECS.		VI -30 SECS.
DAY	5	6	7	8	9	10	11	12
CURRENT ITENSITY (MILLIAMPS) O-TO-PEAK	0.4	0.4	0.6	0.6	0.6	0.6	0.8	0.8
EXPERIMENT I N = 8 (MEAN No. OF PRESSES PER HALF HOUR)	1041.1	1446.6	171.6	222.1	249.0	352.6	394.1	452.5
EXPERIMENT II N = 4 (MEAN No OF PRESSES PER HALF HOUR)	1154.0	1566.0	174.8	239.0	252.8	279.3	305.0	272.5
COMBINED I & II (MEAN No OF PRESSES PER HALF HOUR)	1078.8	1486.4	172.7	227.8	250.3	328.2	364.4	392.5

DIFFERENT STAGES OF TRAINING IN EXPERIMENTS I AND II , SHOWING CURRENT INTENSITY AND MEAN NUMBER OF BAR PRESSES PER HALF HOUR SESSION.

VI-15 second schedule. At no time did a current increase result in any observable motor side-effects. In ten of the twelve rats, an increase in the number of bar-presses on the VI-15 second schedule accompanied the second current increment (the decrease in the number of bar-presses of the remaining two rats was small).

Table 1 also shows the mean number of bar-presses corresponding to each training stage. Because the "screening" and initial training on the ICS lever (Days 5 and 6), as well as the training on the second bar (Days 7 - 12) were identical for both experiments, the means represent all 12 rats. Table N, in the Appendix, contains the data for individual rats. Inspection of Table 1 shows that the mean number of presses on the ICS bar was considerably greater on the second day (Day 6) of the initial ICS training. The mean number of presses on the permanent bar is seen to increase within both the CRF and the VI-15 second stages of training. In addition, it is observed that the same measure increases between the CRF schedule, the VI-15 second schedule, and the first day of the VI-30 second schedule. At no time during this portion of the training was any "priming" necessary to initiate pressing, either on the ICS bar (Days 5 and 6) or on the permanent bar during subsequent training sessions.

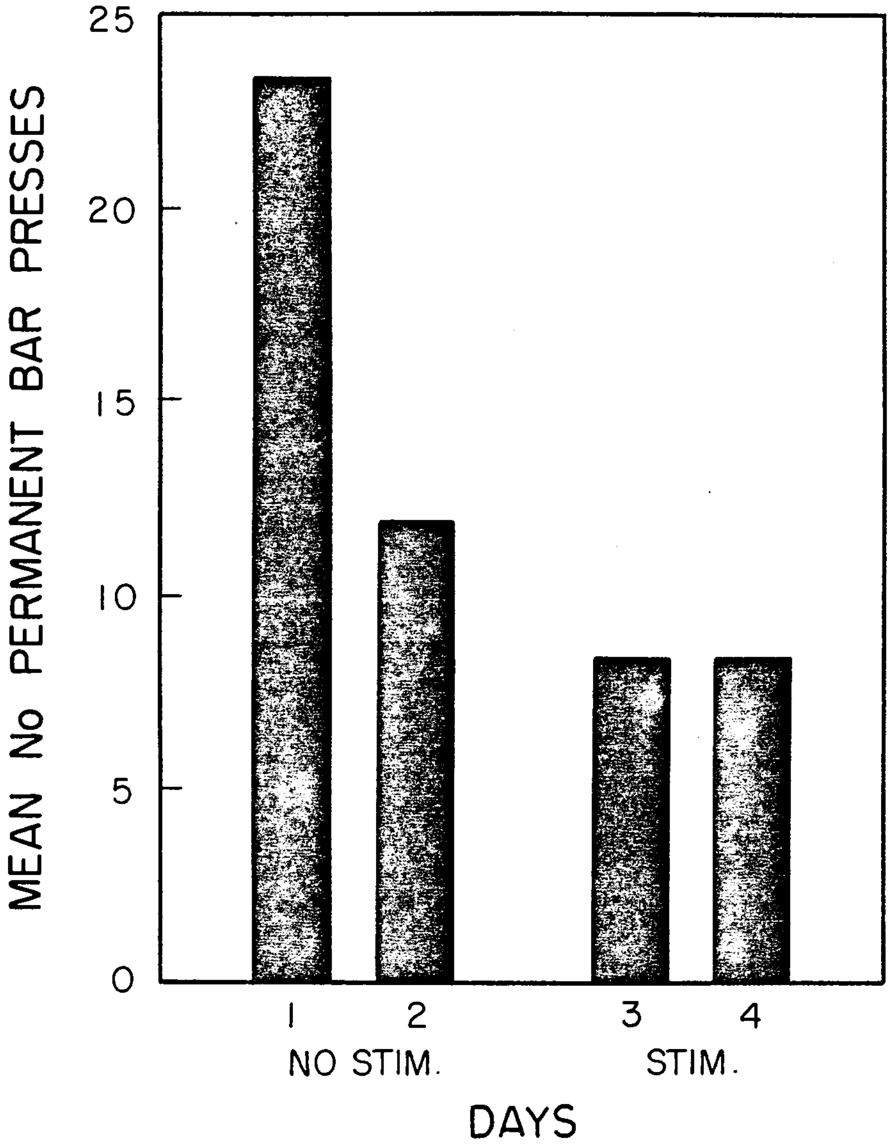
The main method of analysis in the two experiments was the Analysis of Variance with all factors, other than subjects, fixed. Subjects was a random factor which was nested under another factor, the latter factor differing between the different analyses. (Winer, 1962, p. 184). Trend Analyses followed Edwards (1968, p. 287).

Experiment I

Determination of operant levels (Days 1 to 4). Tables A and B (Appendix) present the response measures for individual subjects. The mean number of permanent bar-presses for each of the four sessions of operant level assessment appears in Figure 2. A significant decrease in permanent bar-presses occurred between the two days when neither the Discriminative nor Classically-conditioned stimulus was present, Days 1 vs. 2 ($t = 2.5$, $df = 7$, $p < .05$, within-S, 2-tailed), as shown in Table GG (Appendix). An analysis of variance was performed on the data (Table O, Appendix). A significant decrease ($F = 21.9$, $df = 1/6$, $p < .005$) in the permanent bar-pressing was also observed between the two stimulus conditions, between those days when the Discriminative and Classically-conditioned stimuli were absent (Days 1 & 2) and thoses days when the two stimuli were present (Days 3 & 4).

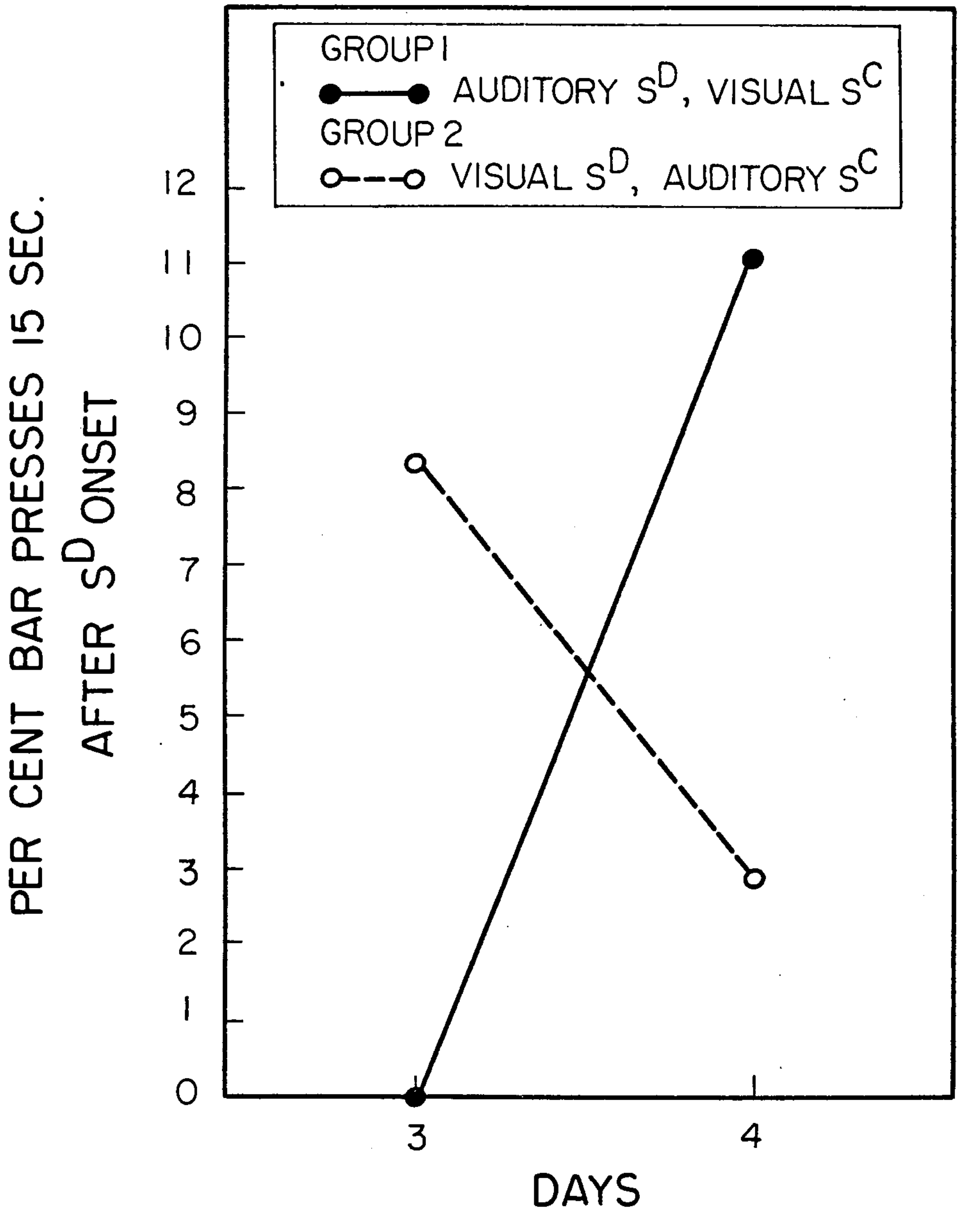
In addition, when the percentage of the permanent bar-presses occurring 15 seconds after the initiation of the Discriminative stimulus was considered for Days 3 and 4 (Table P, Appendix), a significant interaction was observed between the two sessions and the two stimulus groupings ($F = 6.0$, $df = 1/6$, $p < .05$). Figure 3 shows that the post-S^D

FIGURE 2



EXP. I OPERANT BAR PRESSES ON PERMANENT BAR

FIGURE 3



EXP. I PER CENT OPERANT BAR PRESSES ON PERMANENT BAR 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS (GROUPS 1 AND 2) percentage for the group with the auditory Discriminative stimulus and the visual Classically-conditioned stimulus (Group 1) increased considerably from Day 3 to Day 4. In contrast to this increase, the post-S^D percentage for the group with the visual Discriminative stimulus and the auditory Classically-conditioned stimulus (Group 2) decreased over the same period.

Secondary reward training. Tables C and D in the Appendix present data for individual subjects. All rats did not reach both of the criteria which had been set, either on the VI-30 second or the VI-30(50%)-second schedules. Table 2 shows the criteria actually reached by individual rats. A total of four rats reached both criteria under both schedules. Three of these rats were from the group trained with the auditory Discriminative stimulus and the visual Classically-conditioned stimulus (Group 1). The remaining rat was from the group trained with the visual Discriminative stimulus and the auditory Classically-conditioned stimulus (Group 2). The plight of the four rats which did not reach all of the criteria is shown in Table 2. One rat from both Group 1 and Group 2 failed to reach any of the criteria. Rat 8 (Group 2) reached all but the second (discriminability) criterion on the VI-30(50%) schedule. Rat 9 (Group 2) reached neither of the second (discriminability) criteria.

Table 2 also shows the number of pairings of the two experimental stimuli with the ICS, both on the VI-30 and

TABLE 2

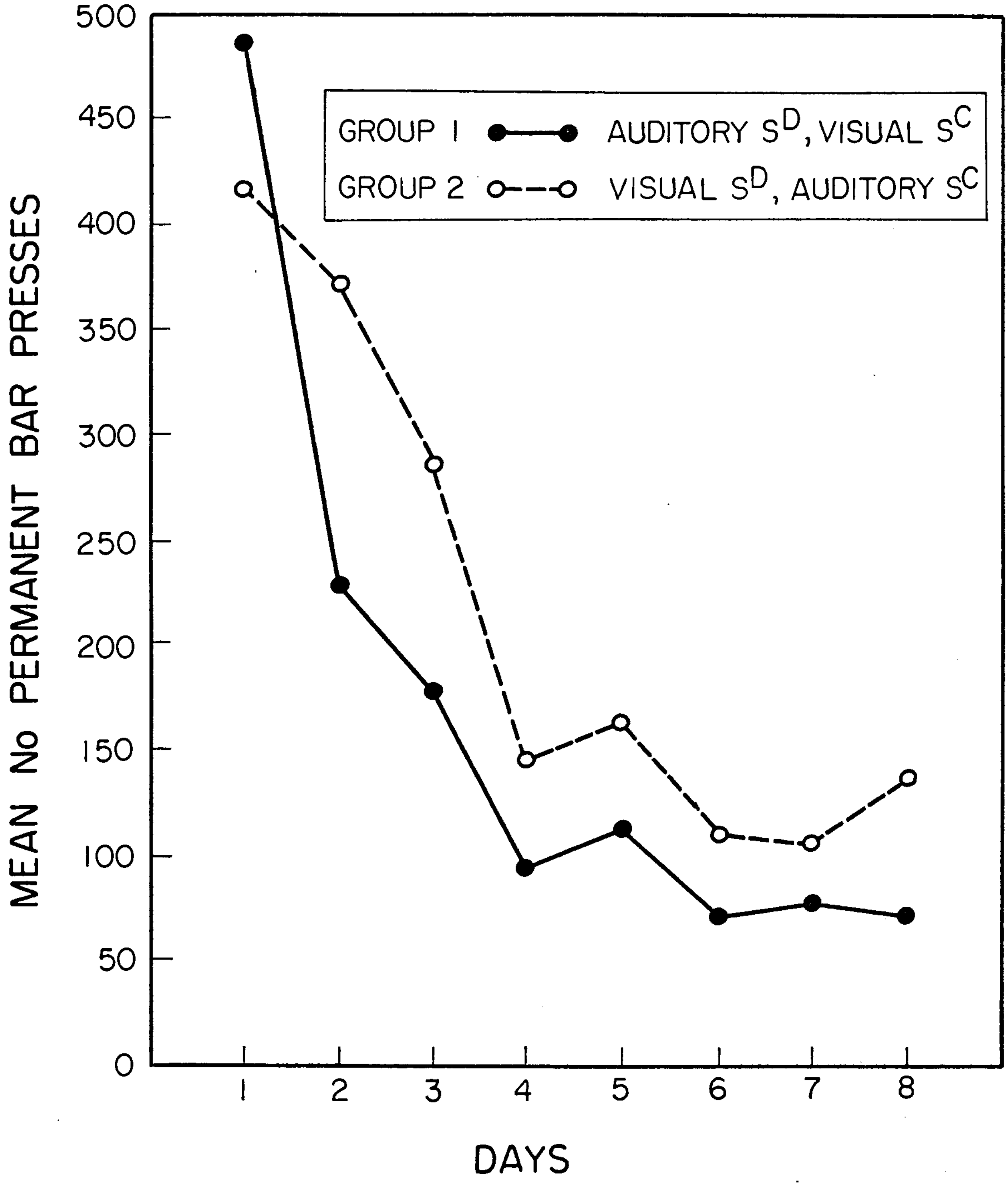
SCHEDULE		VI -30 SECS.			VI -30 SECS. (50%)			No OF STIMULUS-ICS PAIRINGS
		FIRST CRITERION	SECOND CRITERION	NUMBER OF SESSIONS	FIRST CRITERION	SECOND CRITERION	NUMBER OF SESSIONS	
GROUP 1 AUDITORY S^D VISUAL S^C	RAT 3	YES	YES	13	YES	YES	7	743
	RAT 21	YES	YES	17	YES	YES	5	908
	RAT 39	YES	YES	13	YES	YES	6	707
	RAT 6	NO	NO	38	NO	NO	7	1983
GROUP 2 VISUAL S^D AUDITORY S^C	RAT 26	YES	YES	8	YES	YES	6	445
	RAT 8	YES	YES	13	YES	NO	25	1162
	RAT 9	YES	NO	57	YES	NO	5	1862
	RAT 48	NO	NO	16	NO	NO	5	750

EXPERIMENT I - CRITERIA REACHED BY INDIVIDUAL RATS ON VI-30 AND VI-30(50%) SCHEDULES WITH NUMBER OF SESSIONS AND STIMULUS - ICS PAIRINGS INDICATED.

VI-30(50%) schedules. It should be stressed that those rats which did not reach both criteria on one schedule were nevertheless advanced to the next schedule after a reasonable length of time. It is evident from Table 2 that those rats which did not reach criteria accumulated a larger number of stimuli-ICS pairings than those that did reach criteria. In spite of this difference in the number of pairings between individual rats, the mean number of pairings for Group 1 and Group 2 rats were similar (Group 1 = 1085, Group 2 = 1005).

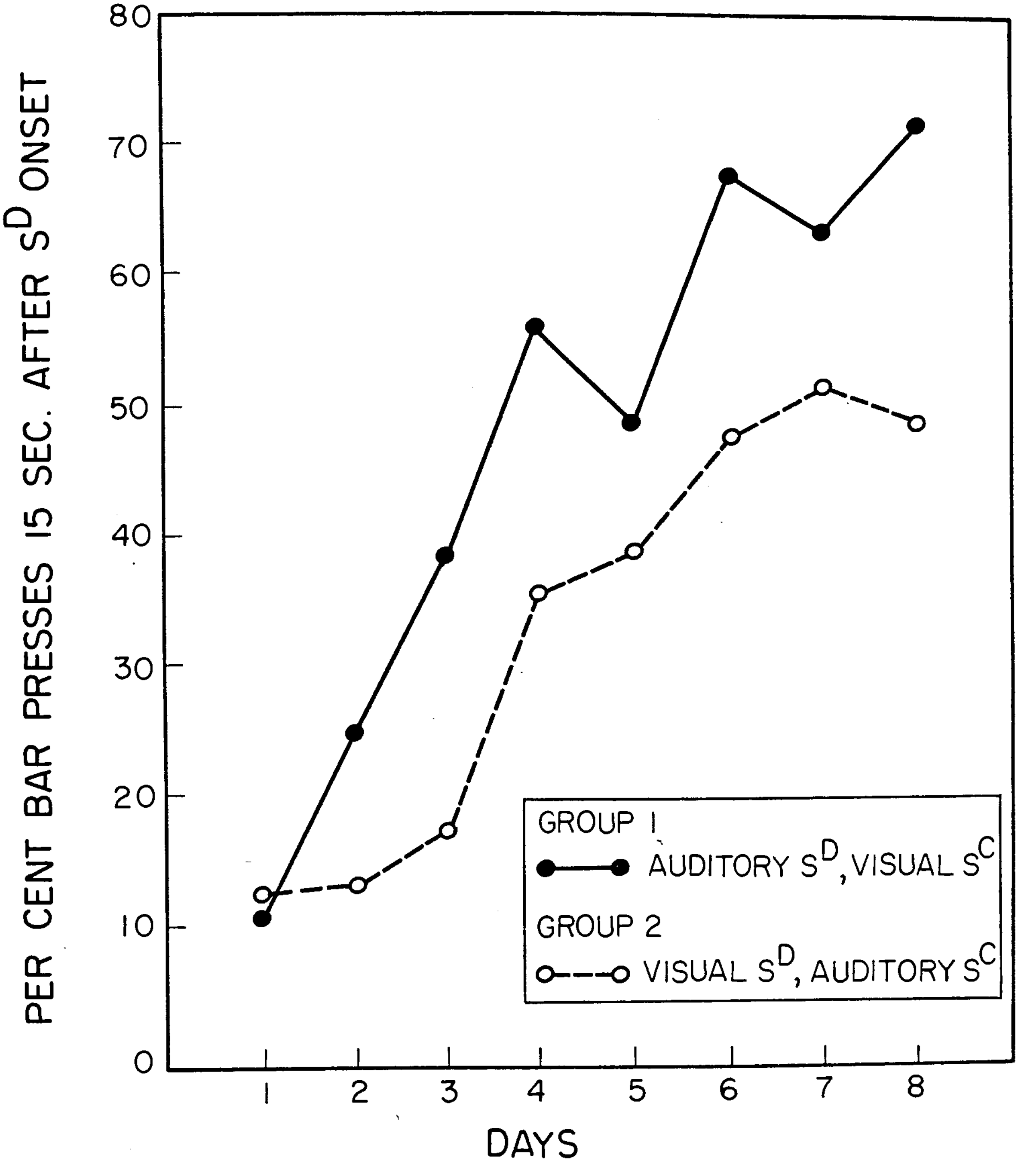
Due to the fact that the minimum number of daily sessions on the VI-30 second schedule before both criteria were reached was 8 (Rat 26), the effect of training on this schedule in the presence of the Discriminative and Classically-conditioned stimuli was measured for all rats over the first eight days. On the first day of this period only the Classically-conditioned stimulus was present. On the subsequent seven days, both the stimuli were present. Figure 4 shows a significant decrease in the mean number of permanent bar presses over the first eight sessions of the VI-30 second schedule (Table Q, Appendix). Although the main effect for sessions was found to be significant (F = 17.4, df = 7/42, $p < .005$), the difference between Group 1 and Group 2 failed to reach significance (F = .92, df = 1/6, $p > .10$). Although the assignment of the auditory and visual stimuli did not have a significant effect, inspection of Figure 4 reveals that the group with the auditory Discriminative stimulus and the visual Classically-conditioned stimulus (Group 1) did show a

FIGURE 4



EXP. I PERMANENT BAR PRESSES DURING FIRST 8 DAYS OF SECONDARY REWARD TRAINING ON VI - 30 SEC. SCHEDULE (GROUPS 1 AND 2)

FIGURE 5



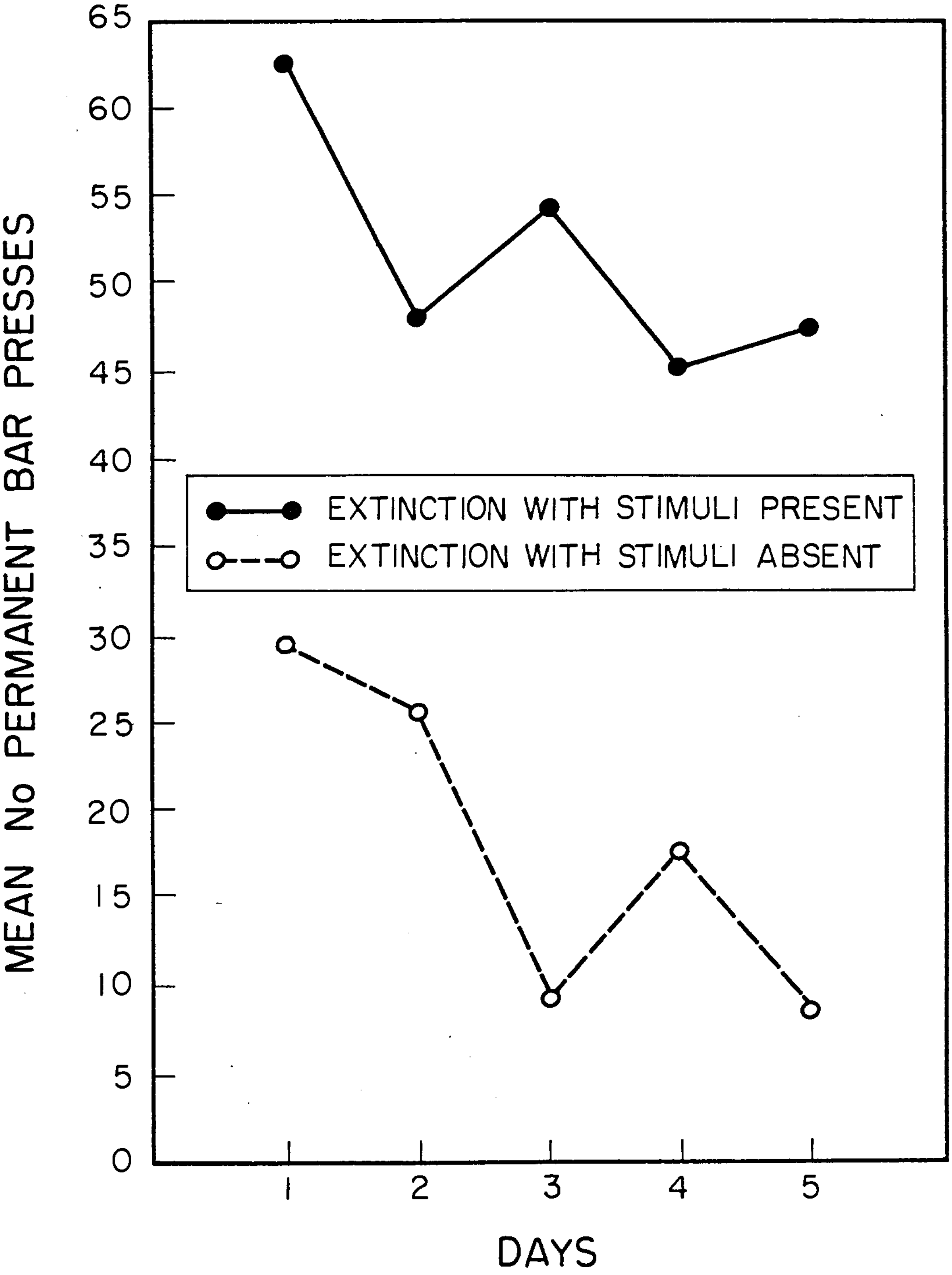
EXP. I PER CENT PERMANENT BAR PRESSES 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS DURING FIRST 8 DAYS OF SECONDARY REWARD TRAINING ON VI-30 SEC. SCHEDULE (GROUPS 1 AND 2) faster decline in the mean number of permanent bar presses over the eight sessions. Figure 5 shows the effect of the same eight training sessions on the post-S^D percentage. Again, the main effect for sessions was significant (F = 17.8, df = 7/42, $p < .005$), the mean percentage of post-S^D responses increasing with subsequent sessions (Table R, Appendix). Although Figure 5 suggests the group trained with the auditory Discriminative stimulus and the visual Classically-conditioned stimulus improved at a faster rate than the group with the reversed modalities, the difference was not significant (F = 1.6, df = 1/6, $p > .10$).

<u>Test for resistance to extinction</u>. The mean number of permanent bar presses that occurred during the first two sessions of extinction condition [2], when the stimuli were absent, was compared to the mean number of permanent bar presses that occurred during the first two days of operant level determination, when the stimuli were also absent (Table AA, Appendix). The mean for the two days of operant level determination was 17.6. The mean for the first two sessions of extinction condition [2] was 26.9. The difference between the two means was significant at the p .05 level, using a within-S t-test (t = 2.4, df = 7, 2-tailed). The mean number of permanent bar presses that occurred in the absence of the experimental stimuli was therefore significantly greater at the start of the extinction phase than before ICS training.

Similarly, the mean number of permanent bar presses that occurred during the first two sessions of extinction condition [1], when the stimuli were present, was compared to the same condition during operant level determination (Table BB, Appendix). In this case, the increase between the operant level situation and the extinction situation was significant at less than the p .001 level, the means being 8.3 and 51.2 respectively (t = 6.3, df = 7, 2-tailed, within-S). The increase in the percentage of permanent bar presses after S^D initiation between the previously mentioned operant and extinction situations was also significant (Table CC, Appendix). The mean percentage of post-S^D responses during Days 3 and 4 of operant level determination was 5.5, while that during the first two days of stimuli-accompanied extinction was 37.1. This difference is significant at the p .001 level (t = 5.4, df = 7, 2-tailed, within-S). It thus appears that both the mean number of permanent bar presses and the percentage of those presses occurring shortly after initiation of the Discriminative stimulus, were greater in the presence of the two stimuli during initial extinction than they were during operant level determination.

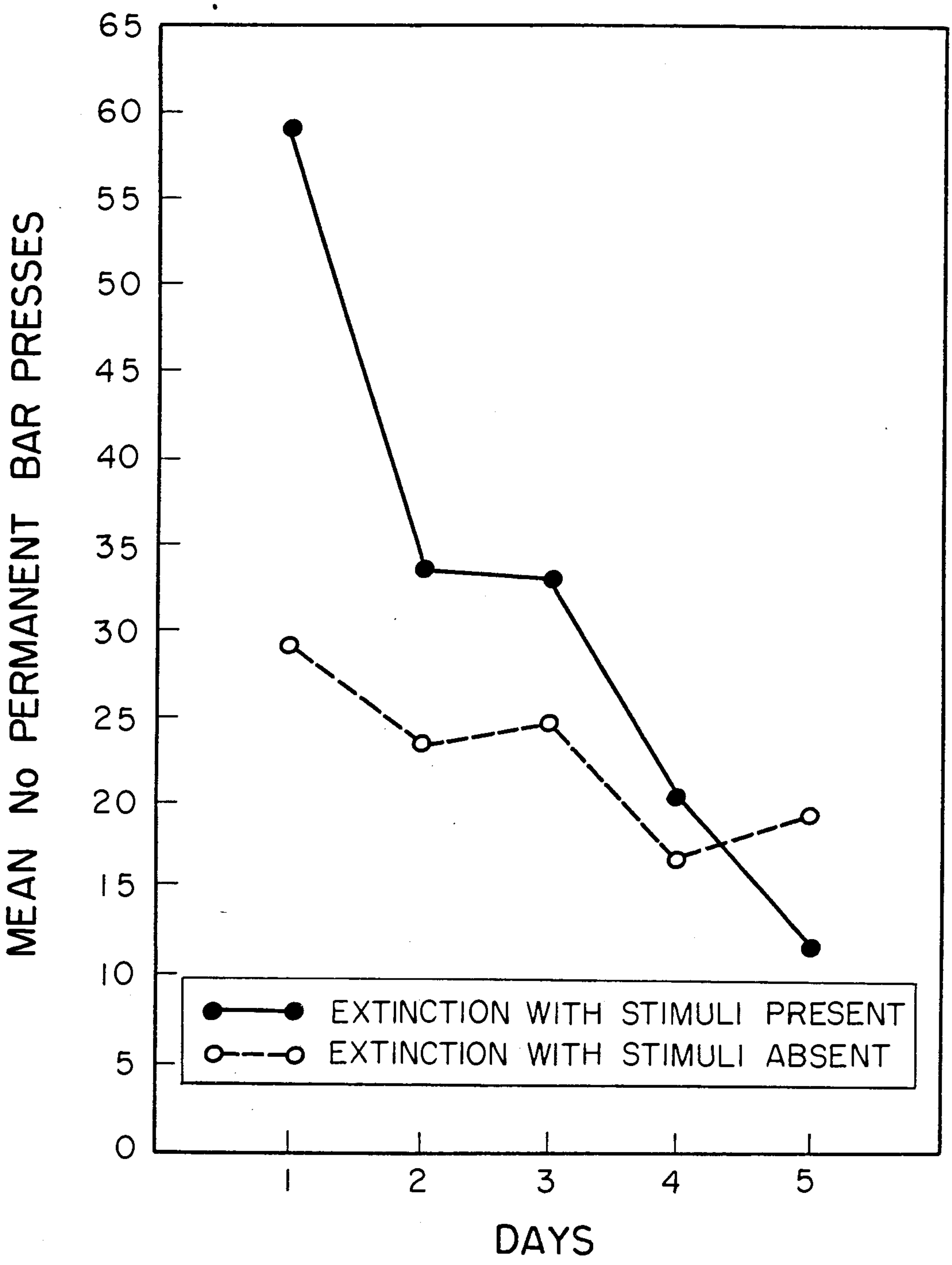
Figures 6 and 7 show the effect of the extinction condition upon the mean number of permanent bar presses over the 5 daily sessions for Groups 1 and 2 respectively. Data for individual subjects appear in the Appendix (Tables E & F). Combining the effect for the group with the auditory

FIGURE 6



EXP. I GROUP I (AUDITORY S^D, VISUAL S^C): PERMANENT BAR PRESSES DURING EXTINCTION WITH AND WITHOUT STIMULI.

FIGURE 7



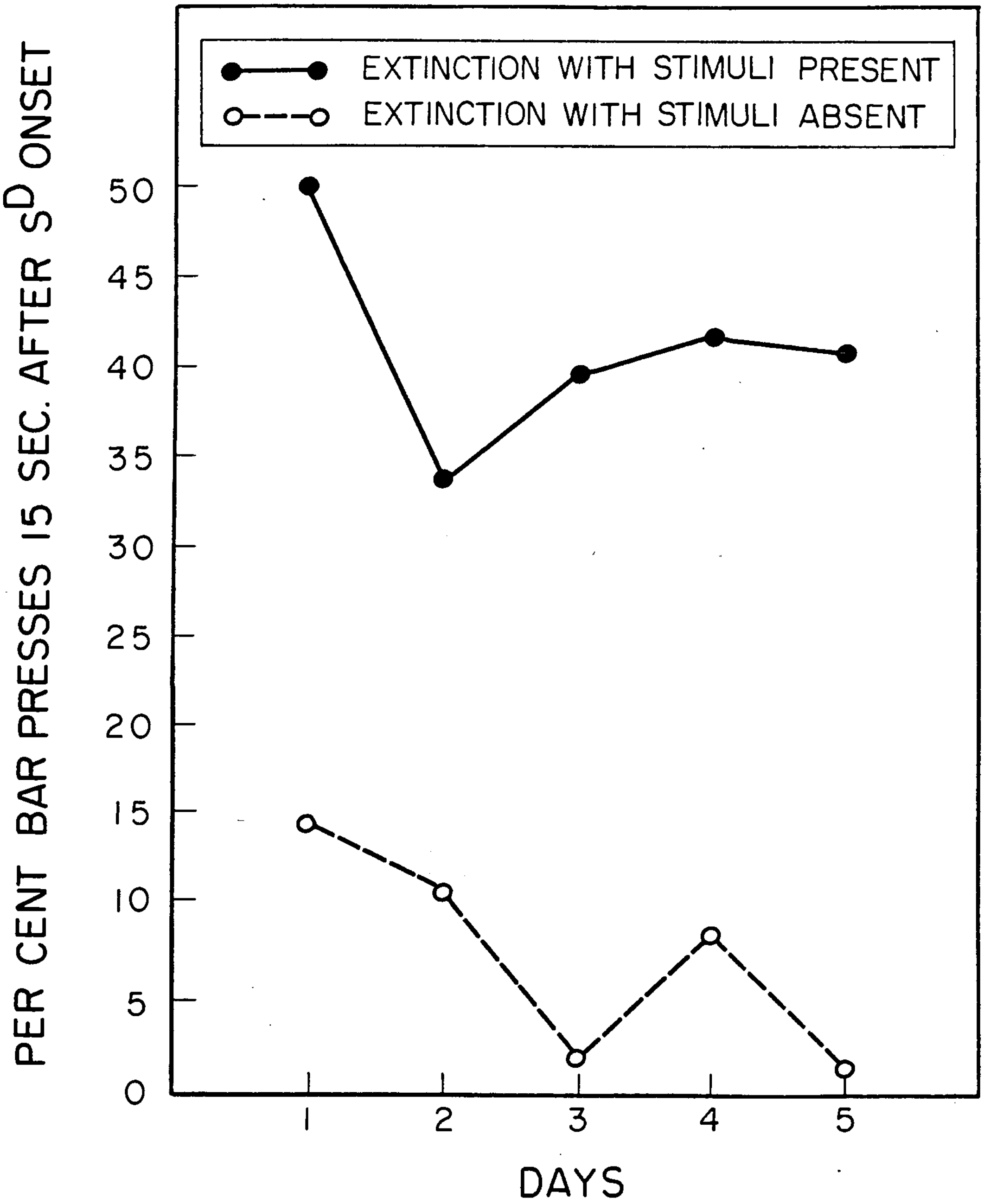
EXP. I GROUP 2 (VISUAL S^D, AUDITORY S^C): PERMANENT BAR PRESSES DURING EXTINCTION WITH AND WITHOUT STIMULI

Discriminative stimulus and the visual Classically-conditioned stimulus with the effect for the group with the reversed modalities (Figures 6 & 7), a significant main effect for extinction condition was found (F = 38.9, df = 1/4, p < .005). The presence of the stimuli produced a significantly greater number of permanent responses. A significant main effect was also observed for sessions, showing that when both extinction conditions (with and without stimuli) are considered for Groups 1 and 2 combined (Figures 6 & 7), a decrement in the mean number of permanent bar responses occurred over the five sessions. Comparing Figure 6 with Figure 7 indicates an interaction existing between the extinction condition and the assignment of stimulus modalities (Groups 1 & 2). This interaction was found to be significant, suggesting that the extinction condition had a greater effect when the Discriminative stimulus was auditory and the Classically-conditioned stimulus was visual than when the modalities were reversed (F = 12.8, df = 1/4, p < .025). Table S in the Appendix shows the summary of the analysis of variance. Trend analysis of the same data showed a significant, over-all, downward linear trend over the extinction sessions (F = 28.8, df = 1/16, p < .01). Analysis of the interactions for linear trend revealed that the interaction between extinction conditions and the assignment of modalities was also significant (F = 5.6, df = 1/16, p < .05). Table HH in the Appendix contains the summary of this analysis of trend.

It appears that the difference between the trends for the two extinction conditions depends on the Group considered. The difference between the trends for the two extinction conditions was greater when the Discriminative stimulus was visual and the Classically-conditioned stimulus was auditory (Figures 6 & 7).

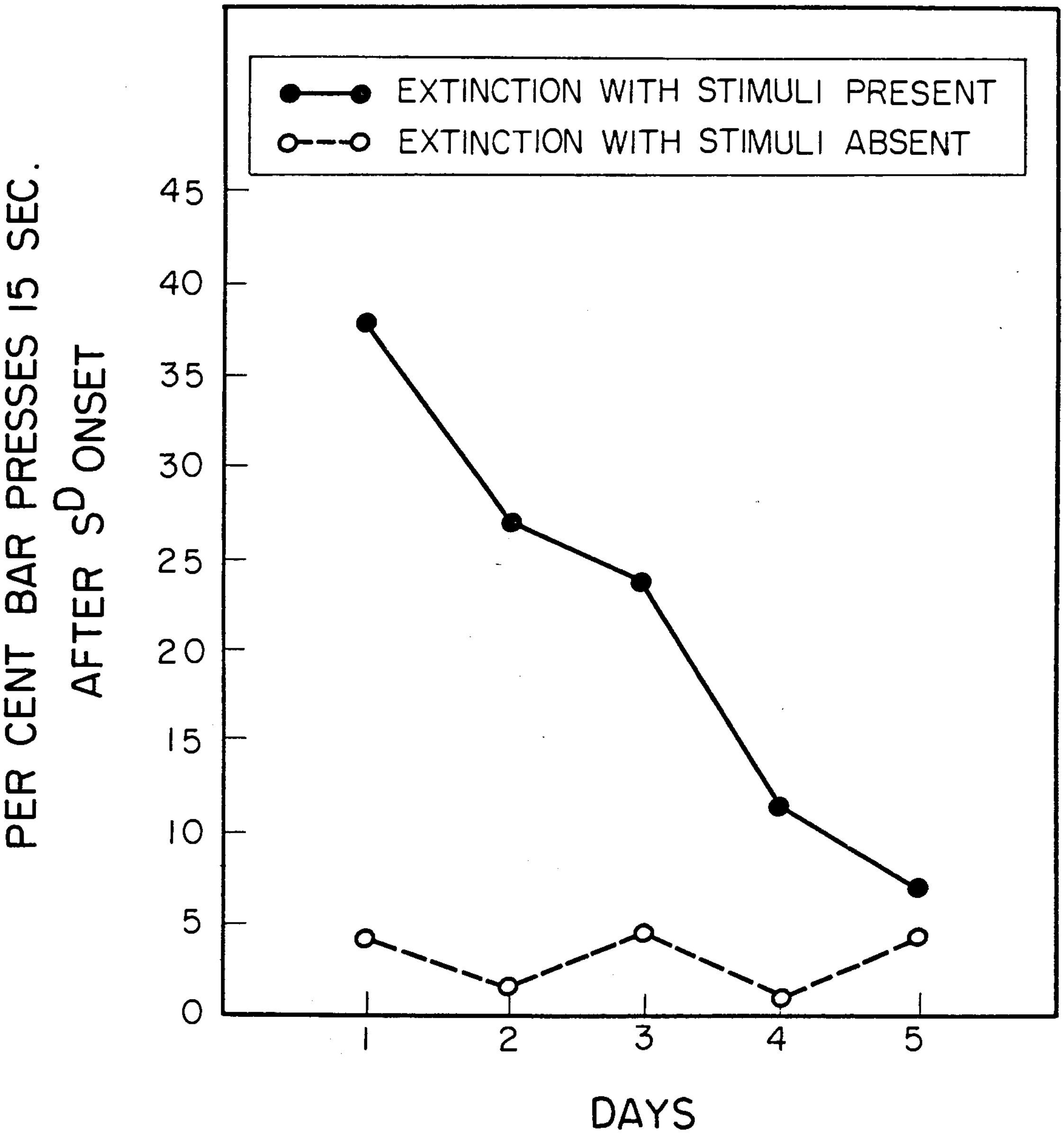
Figures 8 and 9 show the effect of the extinction condition upon the mean percent permanent bar presses occurring 15 seconds after the initiation of the Discriminative stimulus, over the five daily sessions. This effect was found to be significant when both stimulus modality assignments (Groups 1 and 2; Figures 8 & 9) were considered ($F = 183.3$, $df = 1/4$, $p < .005$). The presence of the two experimental stimuli during extinction evidently produced a higher percentage of responses immediately following Discriminative stimulus initiation, compared to the condition where the stimuli were absent. Tables G and H in the Appendix show data for individual subjects. Sessions were also observed to yield a significant main effect ($F = 3.2$, $df = 4/16$, $p < .05$) as was the assignment of stimulus modalities, Group 1 & 2 ($F = 36.9$, $df = 1/4$, $p < .005$). Moreover, a significant interaction was found to exist between Groups, extinction condition, and the session ($F = 3.7$, $df = 4/16$, $p < .05$). This interaction becomes apparent on inspection of Figures 8 and 9. Comparing Figure 8 with Figure 9 indicates that the nature of the extinction condition (with and without stimuli) has a greater effect on

FIGURE 8



EXP. I <u>GROUP I</u> (AUDITORY S^D, VISUAL S^C) : PER CENT PERMANENT BAR PRESSES 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS - EXTINCTION WITH AND WITHOUT STIMULI

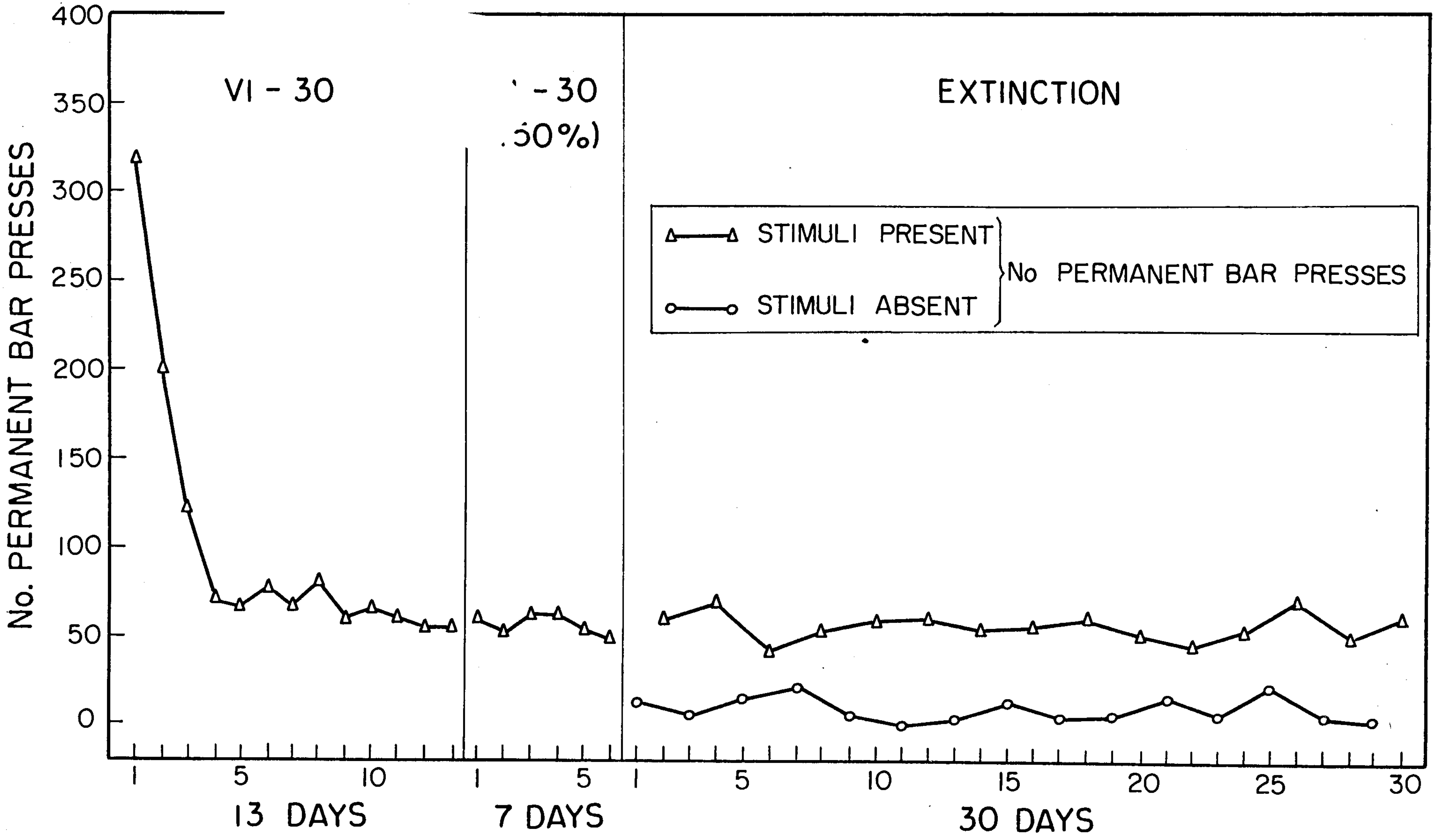
FIGURE 9



EXP. I <u>GROUP 2</u> (VISUAL S^D, AUDITORY S^C) : PER CENT PERMANENT BAR PRESSES 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS - EXTINCTION WITH AND WITHOUT STIMULI the group with the auditory Discriminative stimulus and the visual Classically-conditioned stimulus. This difference of effect between the two stimulus groups increased toward the latter sessions. The summary of the analysis of variance appears in the Appendix (Table T). Trend analysis of this data revealed a significant, over-all, downward linear trend over the daily sessions ($F = 11.4$, $df = 1/16$, $p < .01$). As was the case with the analysis of the number of permanent bar presses, analysis of the interaction for linear trend for the mean percent permanent bar presses occurring 15 seconds after the initiation of the Discriminative stimulus showed a significant interaction between the extinction condition and the Group ($F = 8.68$, $df = 1/16$, $p < .01$). Table HH in the Appendix contains the summary of this analysis. The difference between the trends for the two extinction conditions was greater when the Discriminative stimulus was visual and the Classically-conditioned stimulus was auditory (Figures 8 & 9).

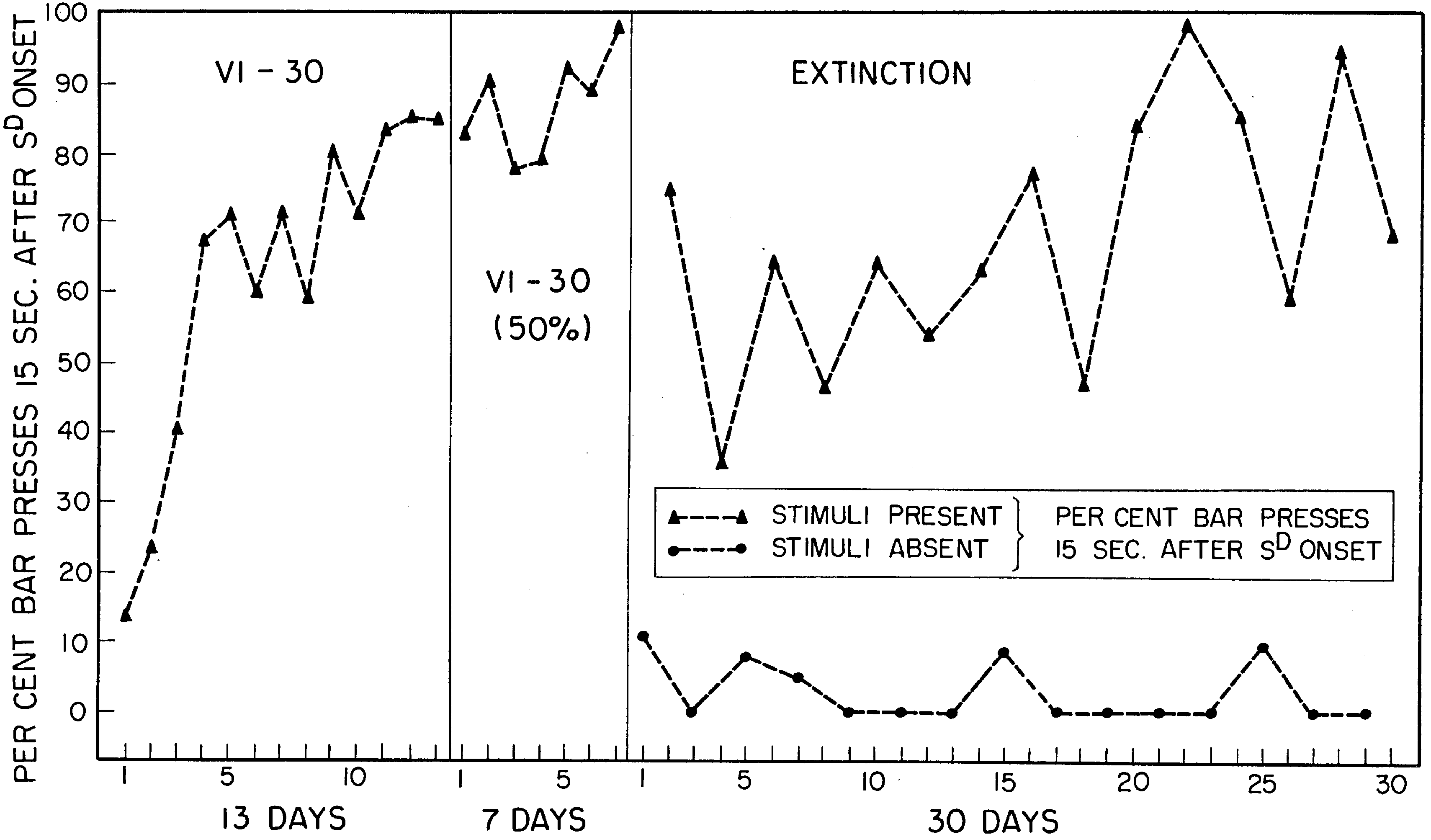
Figures 10 and 11 present the performance of an individual subject, Rat 3, over the secondary reward training and the subsequent extinction. In terms of the hypothesized effects, this subject produced the best performance on both the number of permanent bar presses (Figure 10) and the percentage of presses 15 seconds after the onset of the Discriminative stimulus (Figure 11). In contrast to the other subjects in this experiment who underwent ten extinciton

FIGURE 10



EXP. I - RAT 3. TRAINING WITH STIMULI PRESENT, AND EXTINCTION WITH STIMULI BOTH PRESENT AND ABSENT.

FIGURE 11



EXP. I. - RAT 3. TRAINING WITH STIMULI PRESENT, AND EXTINCTION WITH STIMULI BOTH PRESENT AND ABSENT.

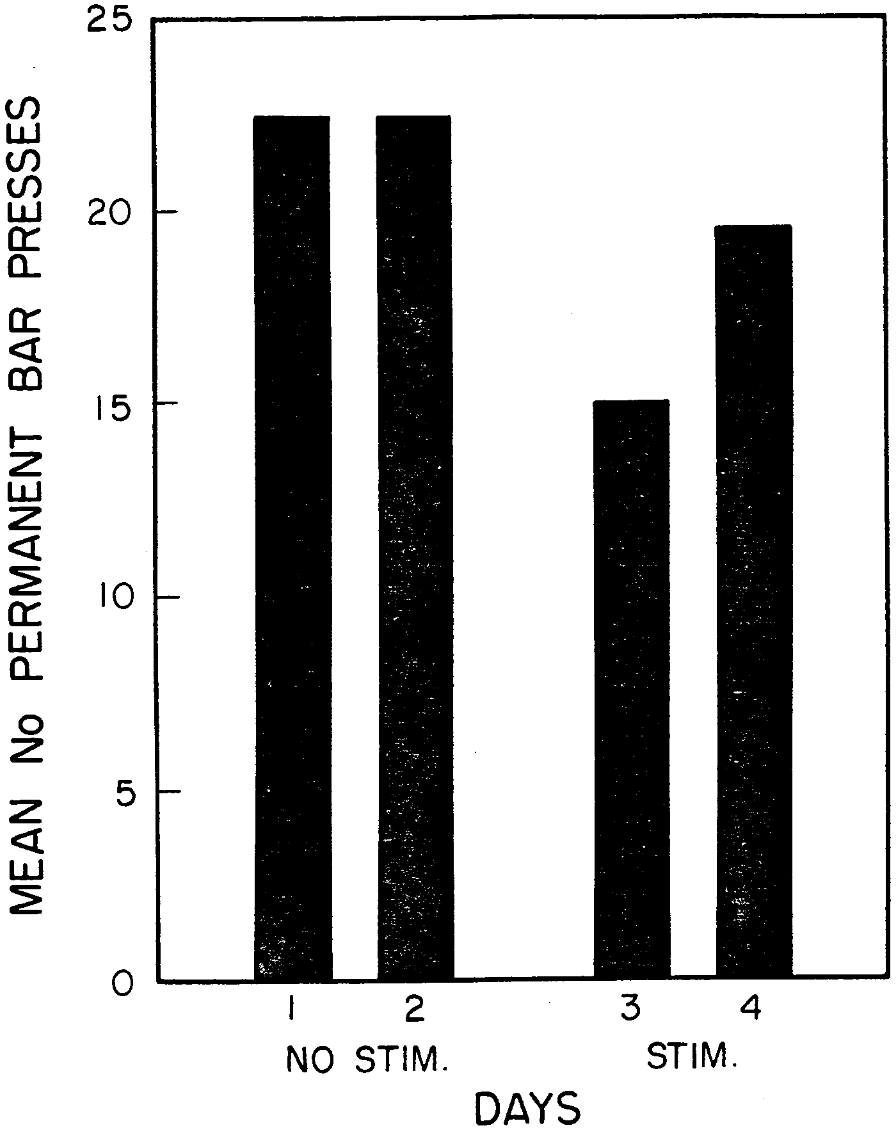
sessions, Rat 3 underwent extinction for a total of 30 days.

Experiment II

Determination of operant levels (Days 1 to 4). Table I in the Appendix shows data for individual subjects. The mean number of permanent bar presses for the four sessions of operant level assessment appear in Figure 12. No significant difference was observed between the permanent bar presses occurring in the absence of the stimulus (Days 1 & 2) and those occurring in the presence of the Classically-conditioned stimulus (Days 3 & 4), ($F = 1.3$, $df = 1/2$, $p > .10$). Table U in the Appendix shows the analysis of variance. In addition, no significant relationships were found when the percentage of the permanent bar-presses occurring 15 seconds after the initiation of the (absent) Discriminative stimulus was considered (Figure 13, Days 3 & 4). The main effect for Days yielded an F value of 5.5 ($df = 1/2$, $p > .10$). The interaction between the two sessions and the two stimulus groups yielded an F value of 4.8 ($df = 1/2$, $p > .10$). Table V (Appendix) shows the analysis of variance for the second dependent measure.

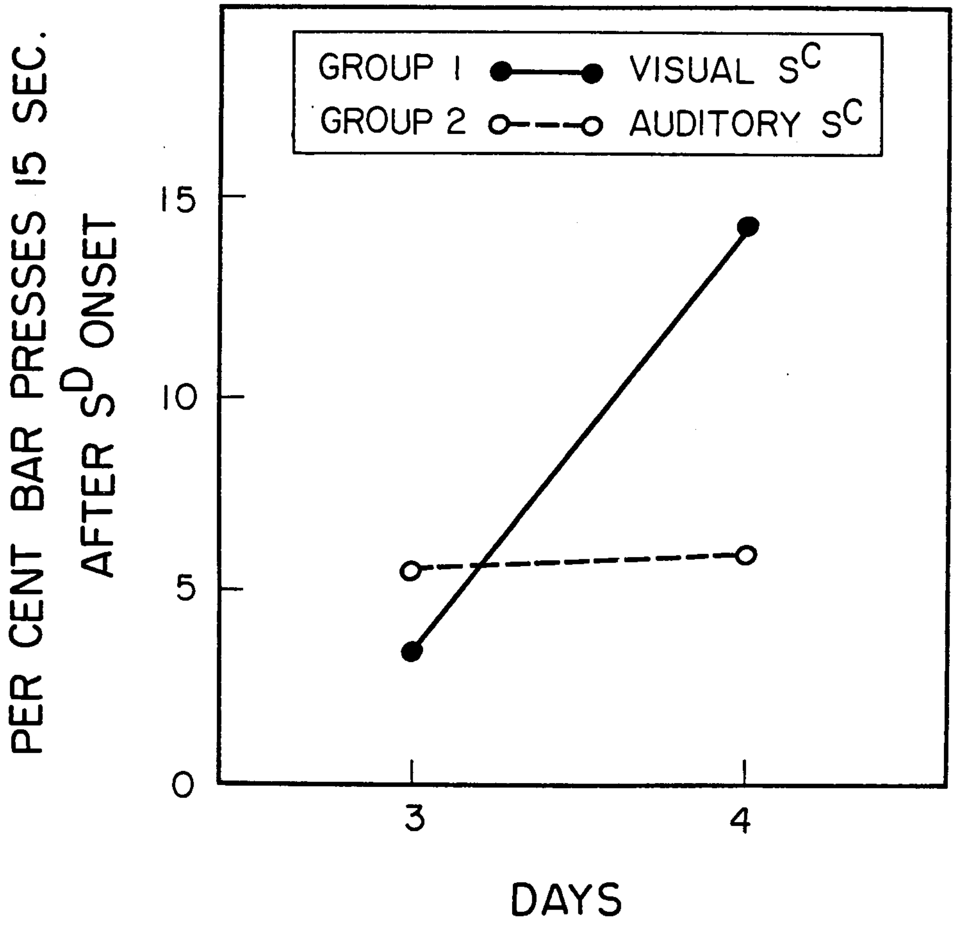
Secondary reward training. Tables J and K in the Appendix present data for individual subjects. All four rats reached the single criterion (stability) of training on both the VI-30 second and the VI-30 second (50%) schedules. Table 3 shows the number of sessions and stimulus-ICS pairings for

FIGURE 12



EXP. II OPERANT BAR PRESSES ON PERMANENT BAR.

FIGURE 13



EXP. II PER CENT OPERANT BAR PRESSES ON PERMANENT BAR 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS (GROUPS 1 AND 2)

TABLE 3

GROUP	RAT	SCHEDULE				TOTAL STIMULUS-ICS PAIRINGS
		VI - 30 SECS.		VI-30 SECS. (50%)		
		SESSIONS	PAIRINGS	SESSIONS	PAIRINGS	
1 VISUAL S^C	45	5	205	5	110	315
	57	10	443	4	88	531
2 AUDITORY S^C	55	5	227	5	103	330
	59	8	348	3	75	423

EXP. II: NUMBER OF SESSIONS AND STIMULUS-ICS PAIRINGS ON VI-30 AND VI-30 (50%) SCHEDULES FOR INDIVIDUAL RATS.

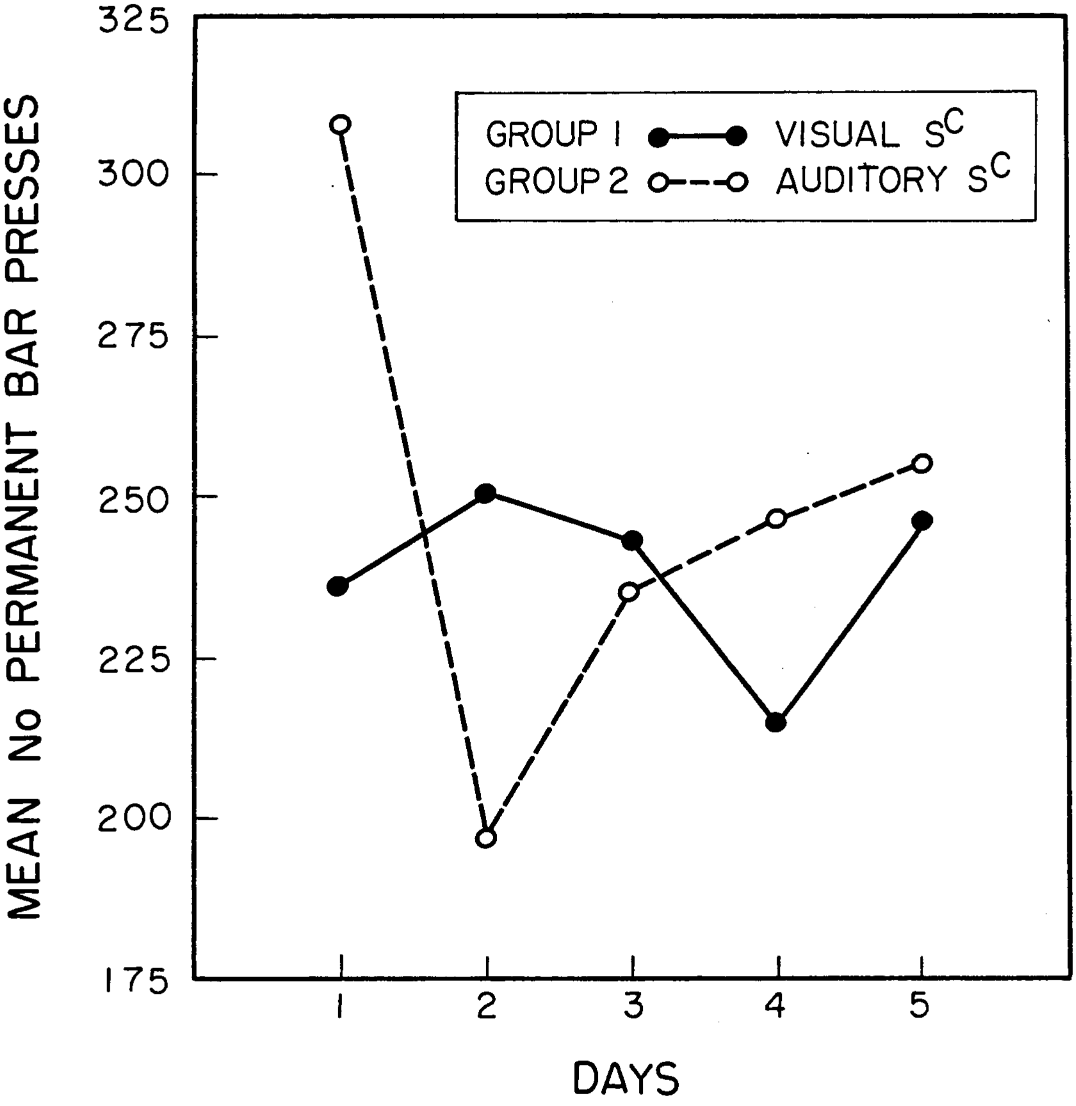
individual rats, on both schedules. The mean number of stimulus-ICS pairings for the group with the visual Classically-conditioned stimulus (Group 1) was 423. The mean number of pairings for the group with the auditory stimulus (Group 2) was 376.5.

Because two rats (45 & 55) reached the training criterion on the VI-30 second schedule within five days, the effect of training with the Classically-conditioned stimulus was measured over the first five days for all of the rats. Figure 14 shows the effect of secondary reward training on the mean number of permanent bar presses. There was no significant variation in permanent bar presses as a function of the five training sessions ($F = 0.58$, $df = 4/8$, $p > .10$). In addition, the modality of the Classically-conditioned stimulus had no significant effect on the mean number of permanent bar presses ($F = .29$, $df = 1/2$, $p > .10$). Table W (Appendix) shows the summary of the analysis of variance.

Figure 15 shows the effect of secondary reward training on the percent permanent bar presses occurring shortly after the initiation of the (absent) Discriminative stimulus. The effect of training on this measure was not significant ($F = 1.0$, $df = 4/8$, $p > .10$), nor was the effect of the stimulus modality ($F = 2.7$, $df = 1/2$, $p > .10$),(Table X, Appendix).

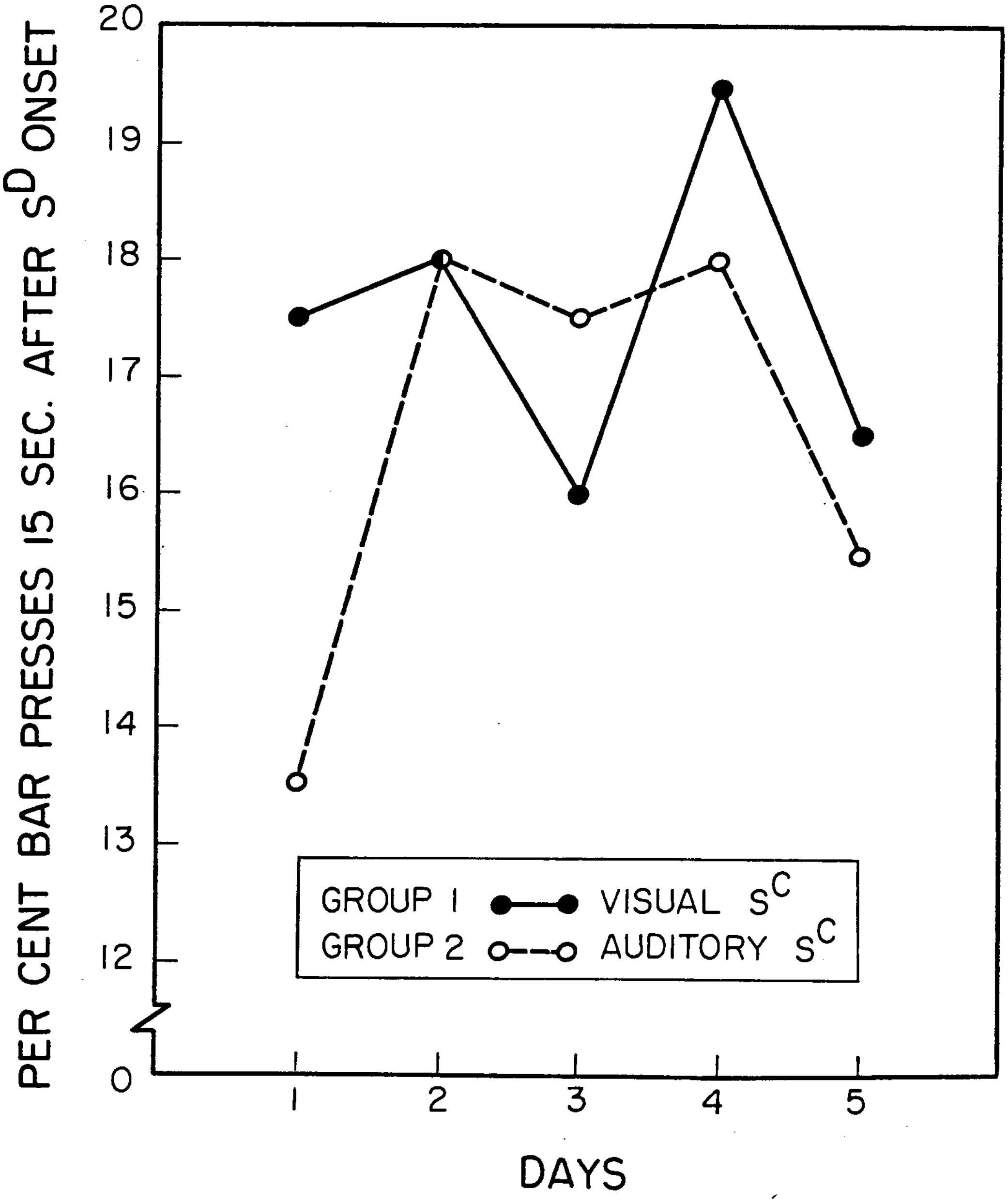
Test for resistance to extinction. Tables L and M in the Appendix show the data for individual subjects. The mean number of permanent bar presses that occurred during the first

FIGURE 14



EXP. II PERMANENT BAR PRESSES DURING FIRST 5 DAYS OF SECONDARY REWARD TRAINING ON VI-30 SEC. SCHEDULE (GROUPS 1 AND 2)

FIGURE 15



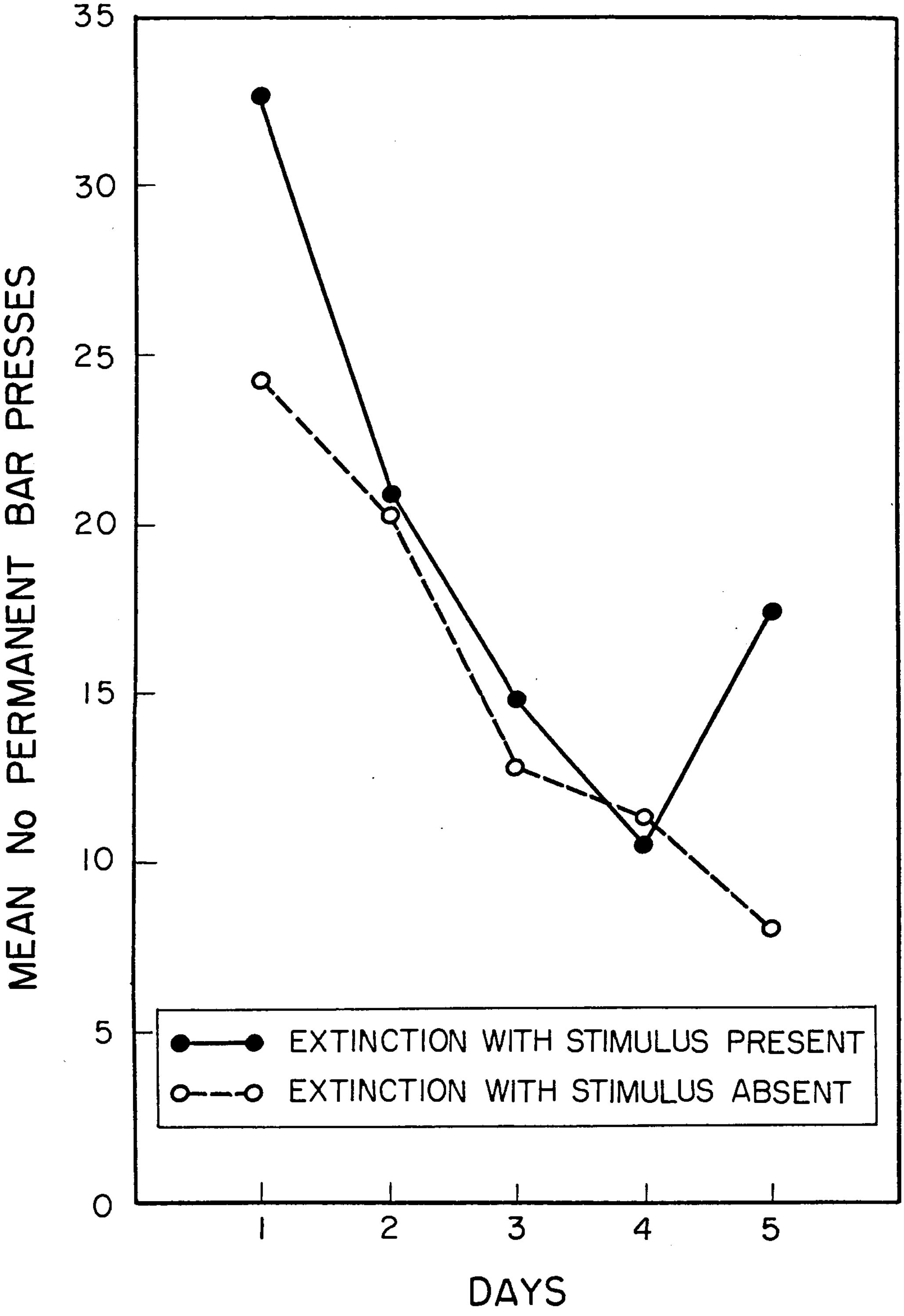
EXP. II PERCENT PERMANENT BAR PRESSES 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS DURING FIRST 5 DAYS OF SECONDARY REWARD TRAINING ON VI-30 SEC. SCHEDULE. (GROUPS 1 AND 2) two sessions of extinction condition [2], when the stimulus was not present, was compared to that occurring during the first two days of operant level determination, when the stimulus was also absent. The mean for the two days of operant level determination was 22.3 as was also the mean for the first two sessions of extinction with the stimulus present. The mean number of permanent bar presses that occurred in the absence of the experimental stimulus was identical before ICS training and at the start of the extinction phase (Table DD, Appendix).

The mean number of permanent bar presses that occurred during the first two sessions of extinction condition [1], when the stimulus was present, was compared to the same condition during operant level determination (Table EE, Appendix). The mean in the first case was 26.9, and that during the operant level determination was 17.3. This increase between the operant and extinction conditions, however, was not significant ($t = 1.4$, $df = 3$, $p > .10$, 2-tailed, within-S). The mean percentage of permanent bar presses immediately after the initiation of the (absent) Discriminative stimulus was determined for Days 3 and 4 of the operant level determination, and also for the first two days of extinction condition [1], during which the stimulus was present (Table FF, Appendix). The two means were 7.4 and 7.1, the difference nonsignificant ($t = 0.2$, $df = 3$, $p > .10$, 2-tailed, within-S).

Figure 16 shows the effect of the extinction condition (with and without stimulus) on the mean number of permanent bar presses over the five daily sessions. The nature of the extinction condition was found to exert no significant effect ($F = .8$, $df = 1/2$, $p > .10$), but there was a significant main effect for sessions, showing a decrement in the mean number of responses as sessions progressed, regardless of the extinction condition ($F = 5.5$, $df = 4/8$, $p < .025$, Table Y, Appendix). Neither the extinction condition ($F = .09$, $df = 1/2$, $p > .10$) nor the daily session ($F = 3.4$, $df = 4/8$, $p > .05$) exerted significant effects on the post-S^D measure, however (Figure 17). Table Z in the Appendix shows the summary of the analysis of variance for the post-S^D measure. Trend analysis of the number of permanent bar presses revealed no significant, over-all, trends over the extinction sessions, both conditions combined (Table HH, Appendix).

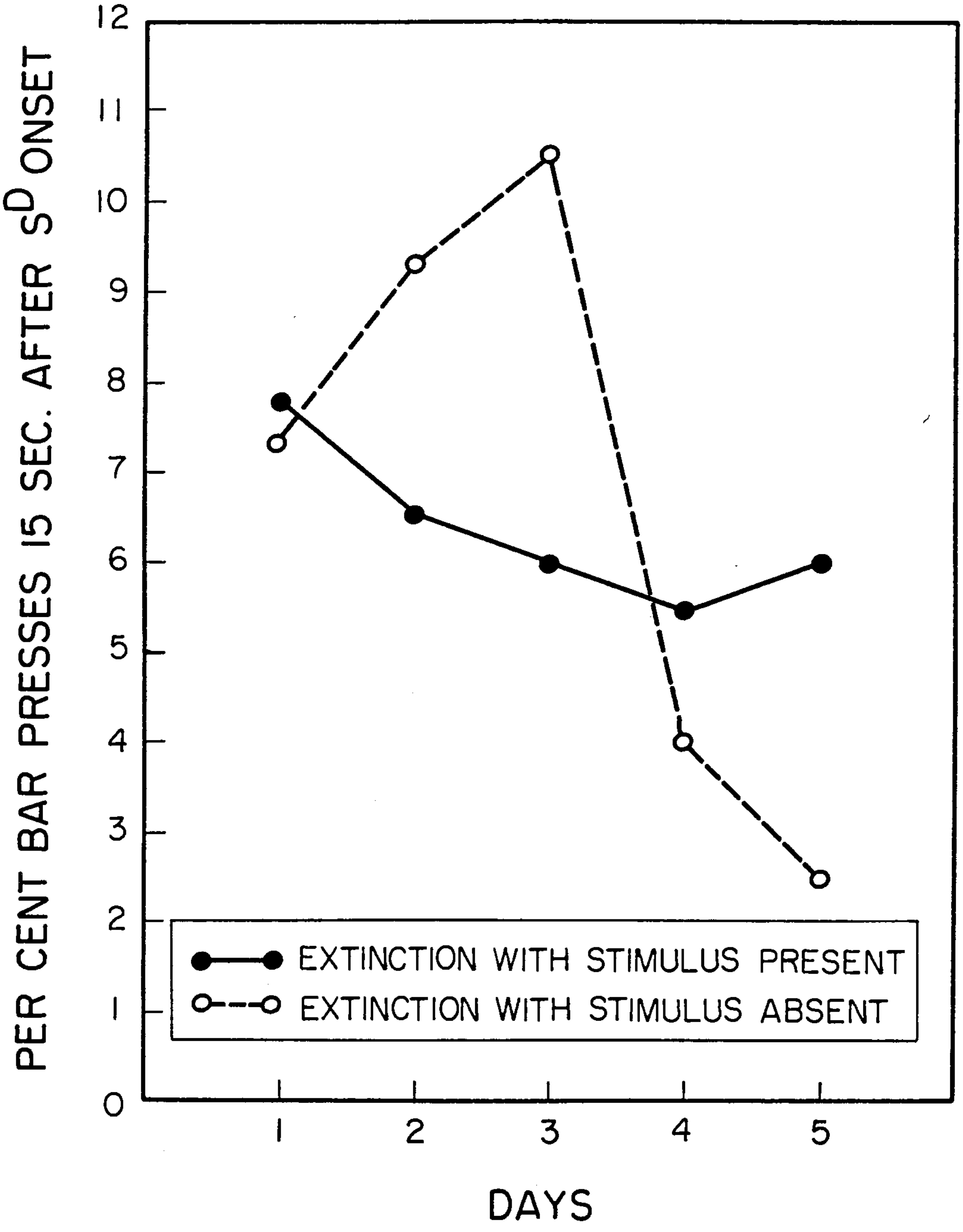
Figures 18 and 19 present the performance of Rat 59 during secondary reward training and subsequent extinction. Comparison of the first and second dependent measures (Figures 18 and 19, respectively) with those of Rat 3 (Figures 10 and 11) illustrates the lack of resistance to extinction in the presence of the stimulus in the second experiment.

FIGURE 16



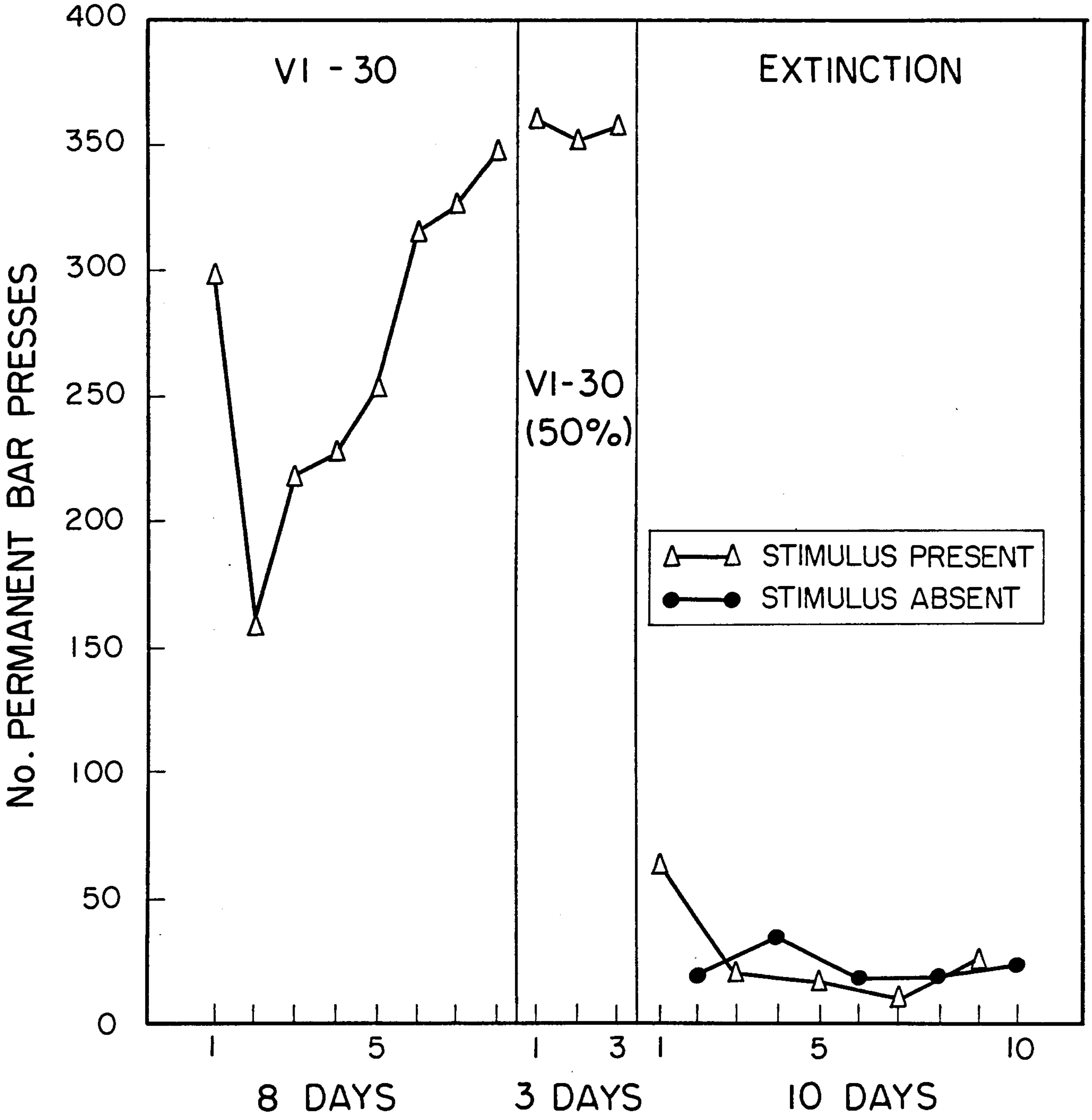
EXP. II PERMANENT BAR PRESSES DURING EXTINCTION WITH AND WITHOUT STIMULUS (GROUPS 1 AND 2 COMBINED)

FIGURE 17



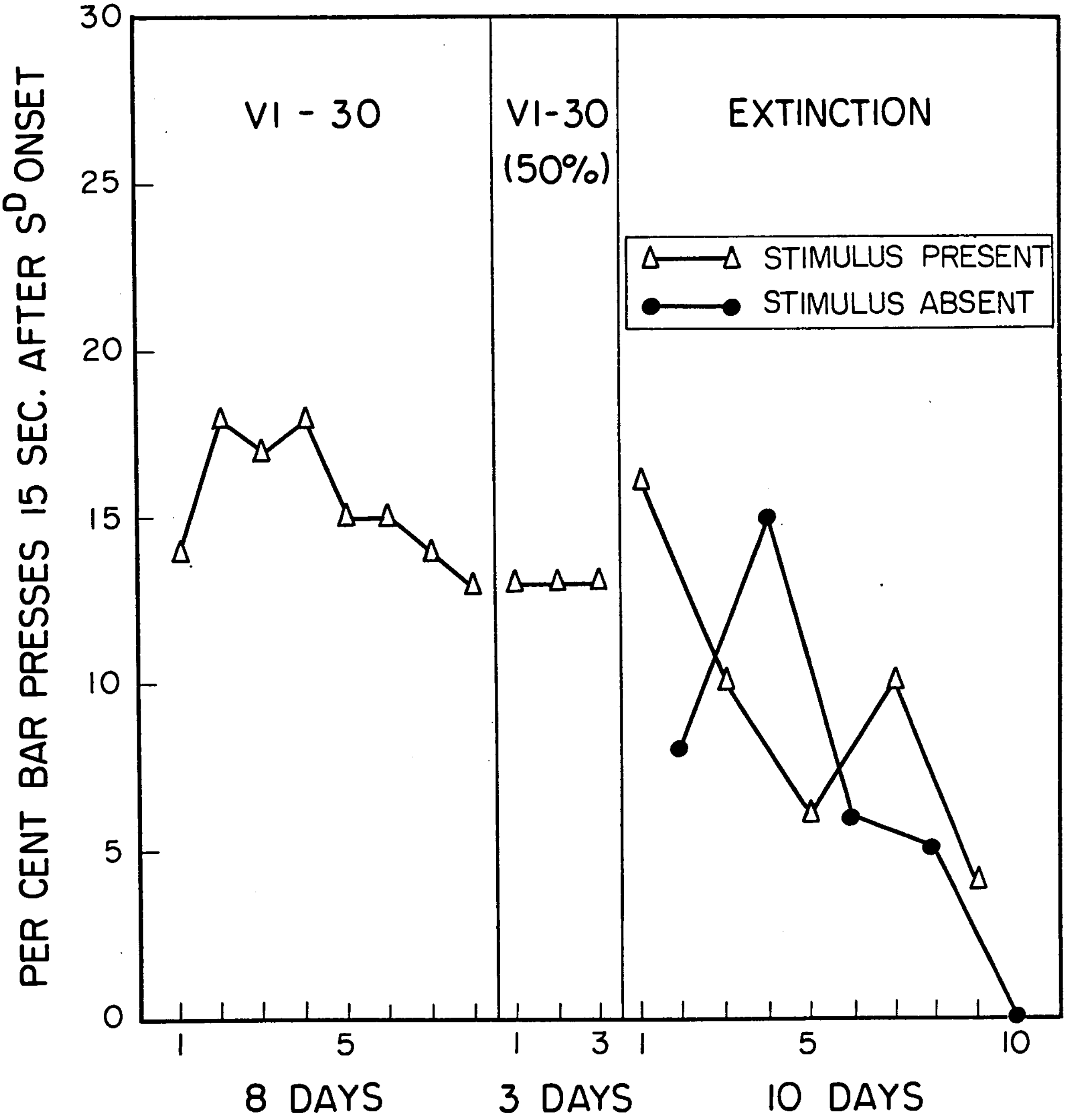
EXP. II PER CENT PERMANENT BAR PRESSES 15 SECS. AFTER ONSET OF DISCRIMINATIVE STIMULUS - EXTINCTION WITH AND WITHOUT STIMULUS. (GROUPS 1 AND 2 COMBINED)

FIGURE 18



EXP. II - RAT 59. PERMANENT BAR PRESSES DURING TRAINING WITH STIMULUS PRESENT, AND EXTINCTION WITH STIMULUS BOTH PRESENT AND ABSENT.

FIGURE 19



EXP. II - RAT 59. PER CENT BAR PRESSES 15 SEC. AFTER S^D ONSET, DURING TRAINING WITH STIMULUS PRESENT, AND EXTINCTION WITH STIMULUS BOTH PRESENT AND ABSENT.

Discussion

Any failure to demonstrate secondary reinforcement through resistance to extinction cannot be attributed to a more fundamental failure to replicate previous results regarding the general nature of ICS-supported responding in the two-lever situation. Although Hawkins and Pliskoff (1964) did not train rats with electrode placements identical to those of the present study, their permanent-bar response rates on a VI-30 second schedule, using similar current intensities, fall within the range of response rates reported in the present study. Thus it appears that the present experiments were successful in at least replicating the phenomena of sustained performance on intermittent schedules characteristic of the 2-bar training paradigm (Hawkins & Pliskoff, 1964; Pliskoff, Wright & Hawkins, 1965).

To adequately demonstrate secondary reinforcement empirically, a number of general relationships should prevail in our present findings. First, there should be some evidence of the neutrality of the experimental stimuli before their association with the opportunity to press for ICS. Response measures during operant level determination should not vary significantly depending on the presence of the experimental stimuli. During extinction, however, the presence of the stimuli should exert a significant effect. Sessions with the experimental stimuli present should yield greater response measures than those sessions with the stimuli absent. In addition, extinction sessions with the stimuli present should produce significantly greater response measures than identical operant level sessions - the result of secondary reward training.

Experiment I satisfies the above requirements with the exception of the first - the lack of unequivocal evidence that both the visual and auditory stimuli were neutral. During operant level assessment, the significant decrease in the number of permanent bar-presses between sessions without the stimuli (Days 1 & 2) and those sessions with the stimuli (Days 3 & 4) may be interpreted in either of two ways. The decline in responding between Days 1 and 2 suggests that the overall decrease between the first two days and the second two days may merely reflect continued habituation to the general experimental situation. On the other hand, the overall decrease might be explained if one or both of the experimental stimuli had been aversive, producing an initial attenuation of on-going behaviour - commonly referred to as "freezing". Compatible with this second hypothesis is the finding of an interaction between the stimulus (Groups 1 & 2) and the latter two sessions of operant level assessment, when the post-S^D percentage of bar-presses is considered. This interaction may indicate that the group with the auditory

Discriminative stimulus (Group 1) partially overcame its initial freezing reaction to the stimulus and learned to terminate the stimulus by pressing the permanent bar. In other words, the termination of the auditory signal may have been reinforcing. Although on Day 4 only eleven percent of the permanent bar-presses followed immediately the initiation of the auditory Discriminative stimulus, subsequent sessions might have extended the upward trend. The slight decrease in the post-S^D measure for the group with the auditory Classically-Conditioned stimulus (Group 2) is also compatible with the presence of an aversive auditory stimulus, the onset of which is negatively reinforcing. At present there is no unequivocal evidence that the auditory and visual stimuli were neutral before their association with the opportunity to obtain ICS. It should be stressed, however, that the aversiveness of one or both of the stimuli is only hypothesized and needs evidence for confirmation. The suggestion that the auditory stimulus may have been aversive, is compatible with significant group differences appearing later in resistance to extinction, but it is not supported by the absence of significant group differences during secondary reward training.

The secondary reward training of Experiment I shows clearly the effect of stimulus control over responding for access to ICS. The significant decrease in permanent bar-presses combined with the significant increase in the percentage of the bar-presses occurring immediately after initiation of the Discriminative stimulus, indicates a progressive inhibition of responding during the period S^D is absent (S^{Δ}).

The extinction phase of Experiment I clearly showed a greater resistance to response decrement in those sessions where the Discriminative and Classically-conditioned stimuli were present. The contribution of the Discriminative stimulus to this resistance is reflected in the post-S^D measure, but the contribution of the Classically-conditioned stimulus cannot be assessed in this experiment. The stimulus control exerted by the Discriminative stimulus - so prominent in secondary reward training - extended well into those extinction sessions where the stimuli were present, but to a considerably greater degree in the case of auditory S^D. In spite of the difference between the two extinction conditions (with and without stimuli), both showed a decrease in responding over the five sessions. The interactions between the extinction conditions and the assignment of stimulus modalities is compatible with the hypothesis that the auditory stimulus had an aversive component, accounting for the greater effect of the extinction conditions for Group 1. In Group 1, rewarding properties of S^D termination may have summated with the discriminated properties of S^D to prolong responding in the presence of the stimuli. It should be noted, however, that the interactions between the extinction conditions and the assignment of stimulus modalities is also compatible with the hypothesis that the auditory stimulus may have had more attentional value independent from any aversive component.

In spite of the possible existence of an aversive Discriminative stimulus, the evidence strongly suggests that the increased resistance to extinction (and the existence of stimulus control) in the presence of the Discriminative and Classically-conditioned stimuli is mainly due to prior association of the stimuli with accessibility to ICS. This tentative conclusion is supported mainly by the existence of the effect for both stimulus modality Groups (1 & 2), and by the evidence of a response decrement over those extinction sessions with the stimuli present (indicating extinction of secondary reinforcement).

In contrast to the findings of Experiment I, those of Experiment II fail to satisfy adequately the requirements necessary to demonstrate secondary reinforcement. It should be stressed here, however, that the small number of subjects (N = 4) and the limited number of stimulus-ICS pairings do not allow an adequate assessment of the ability of a Classically-conditioned stimulus to yield resistance to extinction. Neither operant level assessment nor secondary reward training showed any significant relationships, considering first the mean number of permanent bar-presses and, secondly, the percentage of those presses occurring shortly after the initiation of an (absent) Discriminative stimulus. Two findings during secondary reward training are of some interest, however, when compared to the training phase of Experiment I. The absence of both tendencies present in Experiment I training - those of decreasing permanent bar presses and increasing post-S^D measures - suggest that the presence of the S^D in the first experiment was indeed responsible for response inhibition during S^Δ. The one significant finding of Experiment II, that there was an overall response-decrement effect across extinction conditions and stimuli, is similar to that reported by Seward, Uyeda & Olds (1959). This effect could merely reflect an initial heightened activity level due to previous ICS, and does not even warrant the assignment of secondary rewarding properties to unspecified situational stimuli. Although no firm conclusions can be reached here concerning the ability of a Classically-conditioned stimulus to act as a subsequent secondary reinforcer, the findings of Egger & Miller (1962, 1963) seem pertinent. These authors report that the ease of establishing secondary reinforcement is a positive function of the informational value the stimulus holds for the rat. If this is indeed the case, then an even greater number of stimulus-ICS pairings would be expected to be necessary with the Classically-conditioned stimulus than with the Discriminative stimulus.

In summary, the first experiment does offer strong evidence suggesting that a Discriminative stimulus (and possibly also an accompanying Classically-conditioned stimulus) can operate to produce resistance to extinction, when the stimulus has been previously associated with the opportunity to obtain ICS. The contribution of initially aversive stimuli to the resistance to extinction cannot be ruled out, however, and an appropriate control group could be designed to test this aversiveness hypothesis. The control group would present the Discriminative and Classically-conditioned stimuli on a VI-30 second schedule identical to that in the first experiment, but this schedule would be independent of both the availability of ICS and the subjects' responses. The second experiment, in part due to the small number of subjects and stimulus-reward pairings, unfortunately offers no clear evidence as to whether or not a Classically-conditioned stimulus alone can yield resistance to extinction.

In closing, it should be emphasized that the presence of secondary reinforcement suggested in the first experiment was obtained using a paradigm associating the stimuli with the opportunity to press for ICS (the last response being similar to a normal consummatory response). Other studies attempting to attain secondary reinforcement with MFB-lateral hypothalamus placements have paired the stimuli directly with the bar-press leading to brain stimulation (the consummatory response), and having done so, have failed to demonstrate the secondary reinforcement effect. This state of affairs supports the view that an operant response, antecedent to the response delivering ICS, is necessary when comparing central and peripheral reward.

The present study has been concerned with a paradigm providing delay of reinforcement and response topography similar to that used to establish secondary reinforcement with peripheral reward. Recently, however, studies have shown that the reverse strategy - arranging the peripheral reward paradigm so that it is analagous to that of the classical ICS paradigm - yields similar behavioural phenomena with both types of reward. Panksepp and Trowill (1967a and b) found that the behaviour of rats self-injecting themselves with a highly appetitive solution was similar to that of rats responding for ICS. Fast extinction, priming, and "extinction without responding" were demonstrated. Studies have yet to be conducted demonstrating that secondary reinforcement is <u>unattainable</u> using this intraoral self-injection paradigm, but the evidence suggests that this would be the case.

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Appendix

Table A

Experiment I - Group 1

Response measures during determination of operant levels

RAT	RESPONSE MEASURE	Day 1	Day 2	Day 3	Day 4
3	No. Permanent Bar Presses	9	5	1	7
	Percent Bar Presses 15 Secs. after S^D onset			0	29
21	No. Permanent Bar Presses	50	17	15	13
	Percent Bar Presses 15 Secs. after S^D onset			0	15
39	No. Permanent Bar Presses	24	18	9	5
	Percent Bar Presses 15 Secs. after S^D onset			0	0
6	No. Permanent Bar Presses	12	13	4	6
	Percent Bar Presses 15 Secs. after S^D onset			0	0
Mean	No. Permanent Bar Presses	23.8	13.3	7.3	7.8
Mean	Percent Bar Presses 15 Secs. after S^D onset			0.0	11.0

Table B

Experiment I - Group 2

Response measures during determination of operant levels

RAT	RESPONSE MEASURE	Day 1	Day 2	Day 3	Day 4
26	No. Permanent Bar Presses	20	6	9	8
	Percent Bar Presses 15 Secs. after S^D onset			11	0
8	No. Permanent Bar Presses	11	4	2	2
	Percent Bar Presses 15 Secs. after S^D onset			0	0
9	No. Permanent Bar Presses	17	20	12	7
	Percent Bar Presses 15 Secs. after S^D onset			8	0
48	No. Permanent Bar Presses	44	12	14	18
	Percent Bar Presses 15 Secs. after S^D onset			14	11
Mean	No. Permanent Bar Presses	23.0	10.5	9.3	8.8
Mean	Percent Bar Presses 15 Secs. after S^D onset			8.3	2.8

Table C

Experiment I - Group 1

(Response measures during first 8 days of secondary reward training on VI-30 sec. schedule)

RAT	RESPONSE MEASURE	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8
3	No. Permanent Bar Presses	335	201	121	70	68	78	68	80
	Percent Bar Presses 15 Secs. after S^D onset	13	23	40	67	71	60	71	59
21	No. Permanent Bar Presses	404	96	72	59	83	53	76	50
	Percent Bar Presses 15 Secs. after S^D onset	10	45	65	82	58	89	63	96
39	No. Permanent Bar Presses	312	246	145	112	122	85	71	70
	Percent Bar Presses 15 Secs. after S^D onset	13	18	32	41	39	54	66	67
6	No. Permanent Bar Presses	896	361	273	144	184	74	87	74
	Percent Bar Presses 15 Secs. after S^D onset	5	13	17	34	27	66	54	65
Mean No. Permanent Bar Presses		486.8	226.0	152.8	96.3	114.3	72.5	75.5	73.0
Mean Percent Bar Presses 15 Secs. after S^D onset		10.3	24.8	38.5	56.0	48.8	67.3	63.5	71.8

Table D

Experiment I - Group 2

(Response measures during first 8 days of secondary reward training on VI-30 sec. schedule)

RAT	RESPONSE MEASURE	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8
26	No. Permanent Bar Presses	338	275	224	53	54	47	50	47
	Percent Bar Presses 15 Secs. after S^D onset	13	16	20	64	78	87	88	96
8	No. Permanent Bar Presses	394	275	351	129	126	89	78	82
	Percent Bar Presses 15 Secs. after S^D onset	11	15	13	33	35	52	60	56
9	No. Permanent Bar Presses	713	645	396	235	309	195	169	245
	Percent Bar Presses 15 Secs. after S^D onset	7	7	12	20	16	25	29	20
48	No. Permanent Bar Presses	228	289	181	182	175	134	138	184
	Percent Bar Presses 15 Secs. after S^D onset	18	14	24	24	26	25	29	23
Mean	No. Permanent Bar Presses	418.3	371.0	288.0	149.8	166.0	116.3	108.8	139.5
Mean	Percent Bar Presses 15 Secs. after S^D onset	12.3	13.0	17.3	35.3	38.8	47.3	51.5	48.8

Table E

Experiment I - Group 1

(Permanent Bar Presses during extinction with and without stimuli)

ORDER OF CONDITIONS	RAT	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
WITH-	6	WITH	70	44	60	42	47
		WITHOUT	22	21	9	6	5
WITHOUT	21	WITH	73	53	51	49	54
		WITHOUT	43	52	13	38	23
WITHOUT-	3	WITH	59	69	42	52	58
		WITHOUT	19	4	13	20	4
WITH	39	WITH	49	27	66	40	30
		WITHOUT	31	26	4	7	4
MEAN WITH			62.8	48.3	54.8	45.8	47.3
MEAN WITHOUT			28.8	25.8	9.8	17.8	9.0

Table F

Experiment I - Group 2

(Permanent Bar Presses during extinction with and without stimuli)

ORDER OF CONDITIONS	RAT	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
WITH-WITHOUT	26	WITH	23	16	12	19	11
		WITHOUT	7	15	7	7	5
	8	WITH	57	51	28	15	6
		WITHOUT	16	4	31	7	4
WITHOUT-WITH	9	WITH	103	48	51	22	9
		WITHOUT	55	51	32	26	27
	48	WITH	56	21	42	27	20
		WITHOUT	41	23	29	27	41
MEAN WITH			59.8	34.0	33.3	20.8	11.5
MEAN WITHOUT			29.8	23.3	24.8	16.8	19.3

Table G

Experiment I - Group 1

(Percent permanent bar presses 15 secs. after onset of Discriminative stimulus during extinction with and without stimuli)

ORDER OF CONDITIONS	RAT	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
WITH-WITHOUT	6	WITH	56	45	32	31	13
		WITHOUT	18	14	0	17	0
	21	WITH	30	28	16	37	48
		WITHOUT	12	12	0	11	9
WITHOUT-WITH	3	WITH	75	36	64	46	64
		WITHOUT	11	0	8	5	0
	39	WITH	39	26	47	53	37
		WITHOUT	16	15	0	0	0
MEAN WITH			50.0	33.8	39.8	41.8	40.5
MEAN WITHOUT			14.3	10.3	2.0	8.3	1.8

Table H

Experiment I - Group 2

(Percent permanent bar presses 15 secs. after onset of Discriminative stimulus during extinction with and without stimuli)

ORDER OF CONDITIONS	RAT	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
WITH-WITHOUT	26	WITH	39	19	17	16	18
		WITHOUT	0	0	0	0	0
	8	WITH	51	59	32	0	0
		WITHOUT	0	0	10	0	0
WITHOUT-WITH	9	WITH	34	19	25	18	0
		WITHOUT	14	6	9	0	11
	48	WITH	27	10	21	11	10
		WITHOUT	2	0	0	4	5
MEAN WITH			37.8	26.8	23.8	11.3	7.0
MEAN WITHOUT			4.0	1.5	4.8	1.0	4.0

Table I

Experiment II - Response measures during determination of operant levels

Group 1

RAT	RESPONSE MEASURE	Day 1	Day 2	Day 3	Day 4
57	No. Permanent Bar Presses	19	1	2	8
	Percent Bar Presses 15 Secs. after S^D onset			0	13
45	No. Permanent Bar Presses	15	26	14	31
	Percent Bar Presses 15 Secs. after S^D onset			7	16
Mean	No. Permanent Bar Presses	17.0	13.5	8.0	19.5
Mean	Percent Bar Presses 15 Secs. after S^D onset			3.5	14.5

See Group 2 overleaf..

Table I (continued)

Group 2

55	No. Permanent Bar Presses	22	27	26	22
	Percent Bar Presses 15 Secs. after S^D onset			0	0
59	No. Permanent Bar Presses	33	35	18	17
	Percent Bar Presses 15 Secs. after S^D onset			11	12
Mean No. Permanent Bar Presses		27.5	31.0	22.0	19.5
Mean Percent Bar Presses 15 Secs. after S^D onset				5.5	6.0

Table J

Experiment II - Group 1

Response measures during first 5 days of secondary reward training on VI-30 sec. schedule

RAT	RESPONSE MEASURE	Day 1	Day 2	Day 3	Day 4	Day 5
57	No. Permanent Bar Presses	314	274	229	163	240
	Percent Bar Presses 15 Secs. after S^D onset	14	15	16	23	16
45	No. Permanent Bar Presses	160	227	258	266	254
	Percent Bar Presses 15 Secs. after S^D onset	21	17	16	16	17
Mean	No. Permanent Bar Presses	237.0	250.5	243.5	214.5	247.0
Mean	Percent Bar Presses 15 Secs. after S^D onset	17.5	18.0	16.0	19.5	16.5

Table K

Experiment II - Group 2

Response measures during first 5 days of secondary reward training on VI-30 sec. schedule

RAT	RESPONSE MEASURE	Day 1	Day 2	Day 3	Day 4	Day 5
55	No. Permanent Bar Presses	318	237	255	268	258
	Percent Bar Presses 15 Secs. after S^D onset	13	18	18	18	16
59	No. Permanent Bar Presses	298	157	218	227	252
	Percent Bar Presses 15 Secs. after S^D onset	14	18	17	18	15
Mean	No. Permanent Bar Presses	308.0	197.0	236.5	247.5	255.0
Mean	Percent Bar Presses 15 Secs. after S^D onset	13.5	18.0	17.5	18.0	15.5

Table L

Experiment II - Groups 1 & 2

(Permanent bar presses during extinction with and without stimulus)

GROUP	RAT	ORDER OF CONDITIONS	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
1	57	WITHOUT	WITH	8	34	19	6	8
		-WITH	WITHOUT	41	11	21	19	9
	45	WITH-	WITH	41	14	14	17	16
		WITHOUT	WITHOUT	22	9	6	1	1
2	55	WITHOUT	WITH	19	16	9	9	22
		-WITH	WITHOUT	9	27	6	6	1
	59	WITH-	WITH	63	20	17	10	24
		WITHOUT	WITHOUT	25	34	18	19	21
	MEAN WITH			32.8	21.0	14.8	10.5	17.5
	MEAN WITHOUT			24.3	20.3	12.8	11.3	8.0

Table M

Experiment II - Groups 1 & 2

(Percent permanent bar presses 15 secs. after onset of Discriminative stimulus during extinction with and without stimulus)

GROUP	RAT	ORDER OF CONDITIONS	STIMULUS CONDITION	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
1	57	WITHOUT	WITH	0	9	0	0	0
		-WITH	WITHOUT	7	0	19	11	0
	45	WITH-	WITH	10	7	7	12	6
		WITHOUT	WITHOUT	5	11	17	0	0
2	55	WITHOUT	WITH	5	0	11	0	14
		-WITH	WITHOUT	9	11	0	0	0
	59	WITH-	WITH	16	10	6	10	4
		WITHOUT	WITHOUT	8	15	6	5	0
	MEAN WITH			7.8	6.5	6.0	5.5	6.0
	MEAN WITHOUT			7.3	9.3	10.5	4.0	2.5

Table N

Experiment I -- Number of Bar Presses During Stages of Training

Bar On Which Number of Responses Was Recorded		Retractable (ICS) Bar		Permanent Bar					
Schedule		Continuous		Continuous			VI-15 sec.		VI-30 sec.
Day		5	6	7	8	9	10	11	12
Experiment I	Rat 3	492	1118	84	121	149	125	213	335
	Rat 6	941	1398	138	222	267	587	609	896
	Rat 8	1435	1775	216	138	142	465	496	394
	Rat 9	972	1514	125	260	331	461	720	713
	Rat 21	1470	1482	100	289	224	279	307	404
	Rat 26	1651	1743	133	211	341	369	282	338
	Rat 39	827	1753	426	354	340	280	284	312
	Rat 48	541	790	151	182	198	255	242	228
Experiment II	Rat 45	480	844	99	129	139	153	137	160
	Rat 55	1596	1714	180	162	202	285	281	318
	Rat 57	1492	2114	158	260	291	250	362	314
	Rat 59	1049	1592	262	405	379	429	440	298

Table O

Analysis of Variance -- Experiment I
Number of Permanent Bar Presses
During Operant Level Determination

Source of Variation	df	Mean Square	F
A: Group	1	0.125	0.001
B: Stimulus Condition	1	703.125	21.888**
C: Days	1	264.500	4.795
S: Subjects (w A)	6	230.625	
A X B	1	4.500	0.082
A X C	1	21.125	0.658
B X C	1	264.500	4.008
B X S (w A)	6	55.166	
C X S (w A)	6	32.124	
A X B X C	1	0.500	0.008
B X C X S (w A)	6	66.000	

**Significant at the 0.01 level

Table P

Analysis of Variance -- Experiment I
Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Last Two Days of Operant Level Determination
(arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	0.036	0.212
B: Days	1	0.022	0.196
S: Subjects (w A)	6	0.171	
A X B	1	0.670	6.010*
B X S (w A)	6	0.111	

*Significant at the 0.05 level

Table Q

Analysis of Variance -- Experiment I

Number of Permanent Bar Presses During First 8 Days of Secondary Reward Training on VI-30 sec. Schedule

Source of Variation	df	Mean Square	F
A: Group	1	53015.06	0.920
B: Days	7	130638.60	17.414**
S: Subjects (w A)	6	57629.49	
A X B	7	8709.69	1.161
B X S (w A)	42	7501.84	

**Significant at the 0.01 level

Table R

Analysis of Variance -- Experiment I

Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During First 8 Days of Secondary Reward Training on VI-30 sec. Schedule (arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	1.551	1.589
B: Days	7	1.488	17.825**
S: Subjects (w A)	6	0.976	
A X B	7	0.070	0.835
B X S (w A)	42	0.083	

**Significant at the 0.01 level

Table S

Analysis of Variance -- Experiment I
Number of Permanent Bar Presses During Extinction With and Without Stimuli

Source of Variation	df	Mean Square	F
A: Group	1	1178.112	2.542
B: Stimulus Condition	1	9095.109	38.882**
C: Trials	4	1300.074	7.852**
D: Order of Stimulus Conditions	1	838.513	1.809
A X B	1	2989.012	12.778*
A X C	4	118.735	0.717
A X D	1	3934.011	8.487*
B X C	4	230.731	1.753
B X D	1	19.012	0.081
C X D	4	72.949	0.441
S: Subjects (w AXD)	4	463.535	
A X B X C	4	297.312	2.259
A X B X D	1	234.583	1.003
A X C X D	4	169.261	1.022
B X C X D	4	41.767	0.317
B X S (w AXD)	4	233.919	
C X S (w AXD)	16	165.568	
A X B X C X D	4	178.316	1.355
B X C X S (w AXD)	16	131.584	

* Significant at the 0.05 level

Table T

Analysis of Variance -- Experiment I

Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Extinction With and Without Stimuli (arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	2.614	36.896**
B: Stimulus Condition	1	13.028	183.266**
C: Trials	4	0.422	3.170*
D: Order of Stimulus Conditions	1	0.125	1.762
A X B	1	0.464	6.526
A X C	4	0.140	1.048
A X D	1	0.002	0.027
B X C	4	0.073	0.813
B X D	1	0.009	0.121
C X D	4	0.102	0.767
S: Subjects (w AXD)	4	0.071	
A X B X C	4	0.332	3.719*
A X B X D	1	1.115	15.683*
A X C X D	4	0.110	0.826
B X C X D	4	0.108	1.207
B X S (w AXD)	4	0.071	
C X S (w AXD)	16	0.133	
A X B X C X D	4	0.040	0.451
B X C X S (w AXD)	16	0.089	

* Significant at the 0.05 level

** Significant at the 0.01 level

Table U

Analysis of Variance -- Experiment II

Number of Permanent Bar Presses During Operant Level Determination

Source of Variation	df	Mean Square	F
A: Group	1	441.000	2.224
B: Stimulus Condition	1	100.000	1.311
C: Days	1	20.250	0.203
S: Subjects (w A)	2	198.250	
A X B	1	49.000	0.643
A X C	1	12.250	0.123
B X C	1	20.250	0.900
B X S (w A)	2	76.250	
C X S (w A)	2	99.999	
A X B X C	1	110.250	4.900
B X C X S (w A)	2	22.499	

Table V

Analysis of Variance -- Experiment II

Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Last Two Days of Operant Level Determination (arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	0.064	0.221
B: Days	1	0.140	5.465
S: Subjects (w A)	2	0.288	
A X B	1	0.123	4.823
B X S (w A)	2	0.026	

Table W

Analysis of Variance -- Experiment II

Number of Permanent Bar Presses During First 5 Days of Secondary Reward Training on VI-30 sec. Schedule

Source of Variation	df	Mean Square	F
A: Group	1	530.450	0.288
B: Days	4	1455.699	0.581
S: Subjects (w A)	2	1844.048	
A X B	4	2143.693	0.856
B X S (w A)	8	2505.047	

Table X

Analysis of Variance -- Experiment II

Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During First 5 Days of Secondary Reward Training on VI-30 sec. Schedule (arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	0.001	2.683
B: Days	4	0.004	1.006
S: Subjects (w A)	2	0.000	
A X B	4	0.004	0.959
B X S (w A)	8	0.004	

Table Y

Analysis of Variance -- Experiment II

Number of Permanent Bar Presses During Extinction With and Without Stimulus

Source of Variation	df	Mean Square	F
A: Group	1	84.099	0.194
B: Stimulus Condition	1	160.000	0.800
C: Trials	4	422.162	5.493*
S: Subjects (w A)	2	433.850	
A X B	1	0.900	0.004
A X C	4	45.037	0.586
B X C	4	43.812	0.359
B X S (w A)	2	200.048	
C X S (w A)	8	76.848	
A X B X C	4	213.836	1.754
B X C X S (w A)	8	121.921	

*Significant at the 0.05 level

Table Z

Analysis of Variance -- Experiment II

Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Extinction With and Without Stimulus (arcsine transformation)

Source of Variation	df	Mean Square	F
A: Group	1	0.019	0.084
B: Stimulus Condition	1	0.014	0.091
C: Trials	4	0.149	3.366
S: Subjects (w A)	2	0.233	
A X B	1	0.087	0.581
A X C	4	0.048	1.085
B X C	4	0.099	0.922
B X S (w A)	2	0.149	
C X S (w A)	8	0.044	
A X B X C	4	0.164	1.509
B X C X S (w A)	8	0.108	

Table AA

T Test -- Experiment I

Mean Number of Permanent Bar Presses During First 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days Without Stimuli

Subject No.	First 2 Operant Days	First 2 Extinction Days Without Stimuli
3	7.0	11.5
21	33.5	47.5
39	21.0	28.5
6	12.5	21.5
26	13.0	11.0
8	7.5	10.0
9	18.5	53.0
48	28.0	32.0
Mean	17.6	26.9

df = 7

t = 2.4 Significant at the 0.05 level (2-tailed)

Table BB

T Test -- Experiment I

Mean Number of Permanent Bar Presses During Last 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days With Stimuli

Subject No.	Last 2 Operant Days	First 2 Extinction Days With Stimuli
3	4.0	64.0
21	14.0	63.0
39	7.0	38.0
6	5.0	57.0
26	8.5	19.5
8	2.0	54.0
9	9.5	75.5
48	16.0	38.5
Mean	8.3	51.2

df = 7

t = 6.3 Significant at the 0.001 level (2-tailed)

Table CC

T Test -- Experiment I

Mean Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Last 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days With Stimuli

Subject No.	Last 2 Operant Days	First 2 Extinction Days With Stimuli
3	14.5	55.5
21	7.5	29.0
39	0.0	32.5
6	0.0	50.5
26	5.5	29.0
8	0.0	55.0
9	4.0	26.5
48	12.5	18.5
Mean	5.5	37.1

df = 7

t = 5.4 Significant at the 0.001 level (2-tailed)

Table DD

T Test -- Experiment II

Mean Number of Permanent Bar Presses During First 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days Without Stimulus

Subject No.	First 2 Operant Days	First 2 Extinction Days Without Stimulus
57	10.0	26.0
45	20.5	15.5
55	24.5	18.0
59	34.0	29.5
Mean	22.3	22.3

df = 3

t = 0.0

Table EE

T Test -- Experiment II

Mean Number of Permanent Bar Presses During Last 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days With Stimulus

Subject No.	Last 2 Operant Days	First 2 Extinction Days With Stimulus
57	5.0	21.0
45	22.5	27.5
55	24.0	17.5
59	17.5	41.5
Mean	17.3	26.9

df = 3

t = 1.4

Table FF

T Test -- Experiment II

Mean Percentage of Permanent Bar Presses 15 secs. After Onset of S^D During Last 2 Days of Operant Level Determination Compared to the Same Measure During First 2 Extinction Days With Stimulus

Subject No.	Last 2 Operant Days	First 2 Extinction Days With Stimulus
57	6.5	4.5
45	11.5	8.5
55	0.0	2.5
59	11.5	13.5
Mean	7.4	7.1

df = 3

t = 0.20

Table GG

T Test -- Experiment I

Mean Number of Permanent Bar Presses During First Day of Operant Level Determination Compared to the Same Measure During the Second Day

Subject No.	First Operant Day	Second Operant Day
3	9	5
21	50	17
39	24	18
6	12	13
26	20	6
8	11	4
9	17	20
48	44	12
Mean	23.4	11.9

df = 7

t = 2.5 Significant at the 0.05 level (2-tailed)

Table HH

Trend Analyses -- Extinction Trials, Experiments I and II

Experiment I

Permanent Bar Presses:

linear overall trend (across conditions and Groups)

$D_1 = -873$ (downward trend)

linear component = 4763 with 1 df

$F = 28.8$ (df = 1/16)**

quadratic overall trend (across conditions and Groups)

$D_2 = 235$

quadratic component = 246.5 with 1 df

$F = 1.5$ (df = 1/16)

analysis of interactions for linear trend

Source of Variation	df	Mean Square	F
A: Groups	1	317	1.9
B: Stimulus Condition	1	466	2.8
A X B	1	925	5.6*
error term	16	165.6 (from Table S)	

* Significant at the 0.05 level

** Significant at the 0.01 level

Table HH (continued)

Experiment I

Percent Permanent Bar Presses 15 sec. After Onset of S^D
(arcsine transf.)

linear overall trend (across conditions and Groups)

D_1 = -15.576 (downward trend)

linear component = 1.516 with 1 df

F = 11.4 (df = 1/16)**

quadratic overall trend (across conditions and Groups)

D_2 = 3.970

quadratic component = 0.070 with 1 df

F = 0.53 (df = 1/16)

analysis of interactions for linear trend

Source of Variation	df	Mean Square	F
A: Groups	1	0.056	0.4
B: Stimulus Condition	1	0.170	1.3
A X B	1	1.154	8.7**
error term	16	0.133 (from Table T)	

** Significant at the 0.01 level

Table HH (continued)

Experiment II

Permanent Bar Presses:

linear overall trend (across conditions and Groups)

D_1 = -330 (downward trend)

linear component = 136.1 with 1 df

F = 1.8 (df = 1/8)

quadratic overall trend (across conditions and Groups)

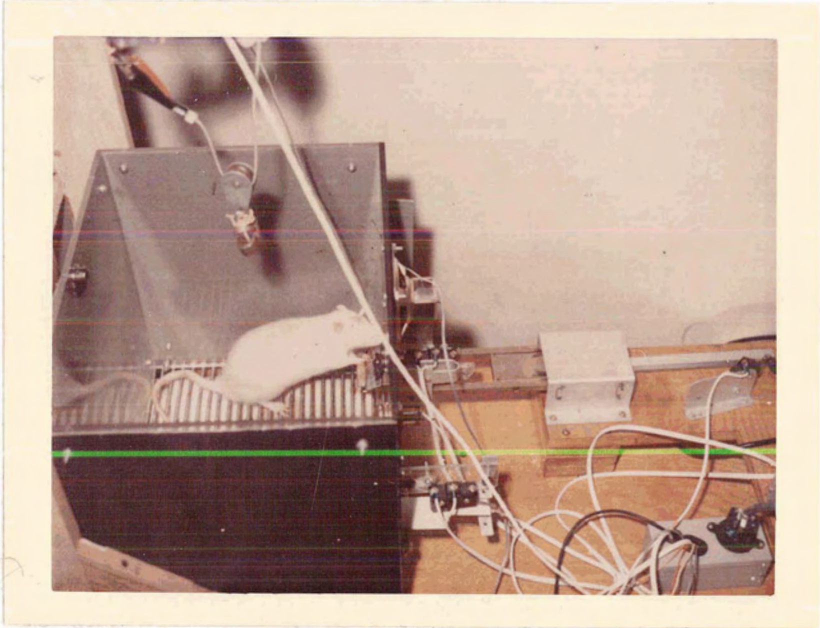
D_2 = 188

quadratic component = 316 with 1 df

F = 4.1 (df = 1/8)

error term = 76.8 with 8 df (from Table Y)

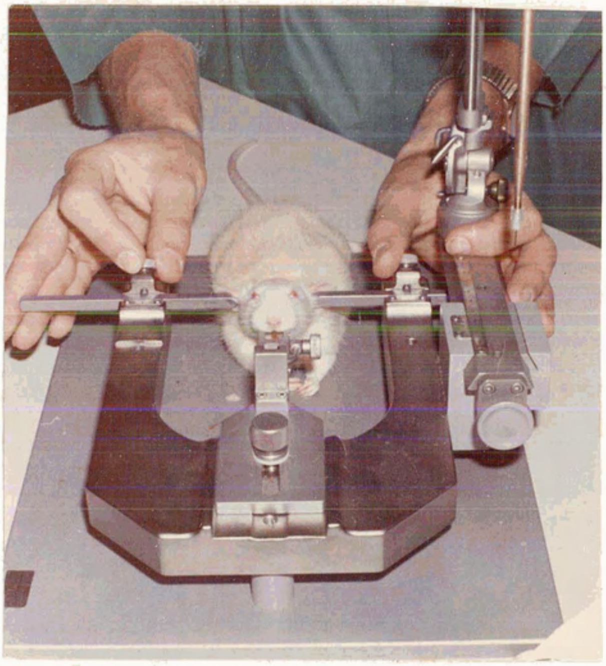
Figure 20



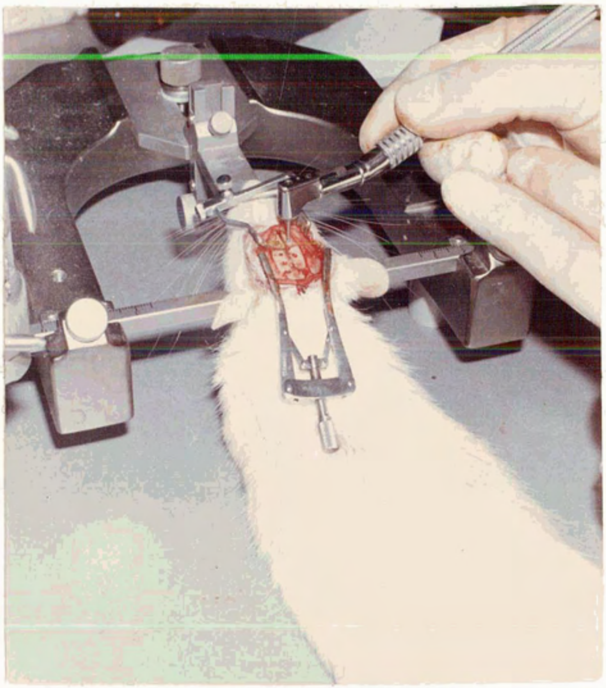
Skinner box designed and constructed by author

Figure 21

Surgical technique

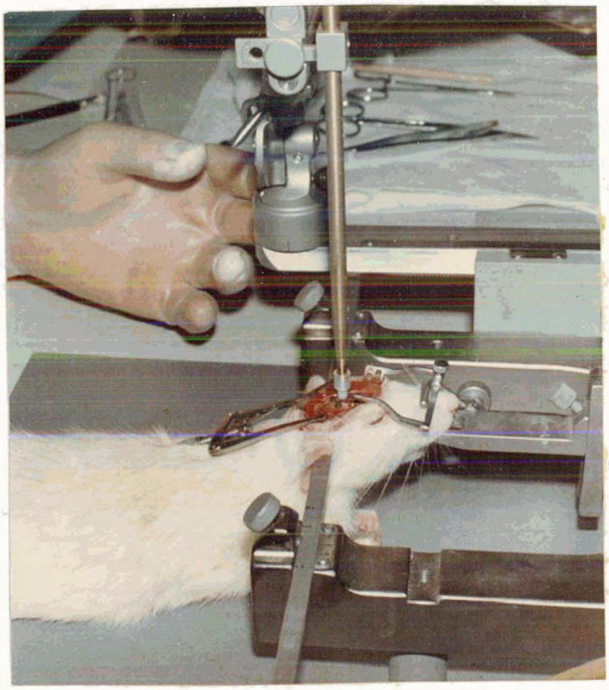


A. Positioning of rat in stereotaxis

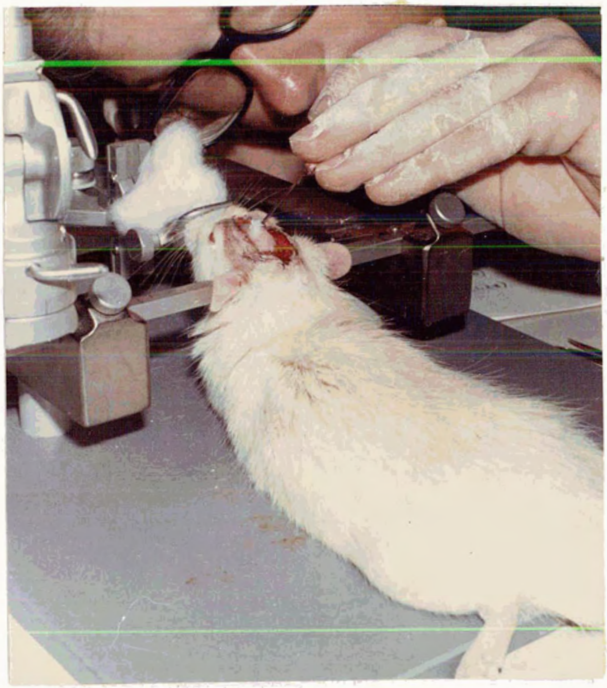


B. Drilling holes for anchoring screws

Figure 21 (continued)



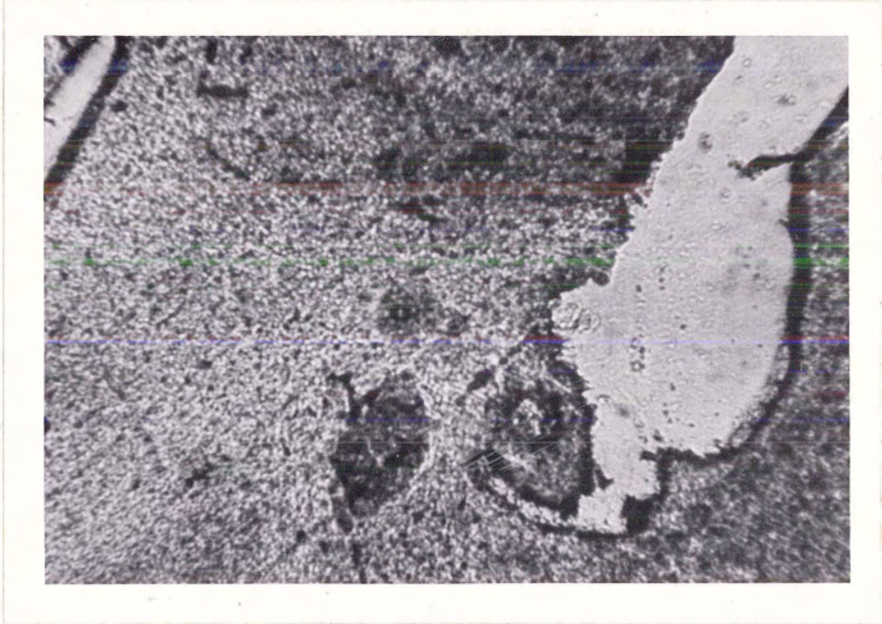
C. Lowering electrode



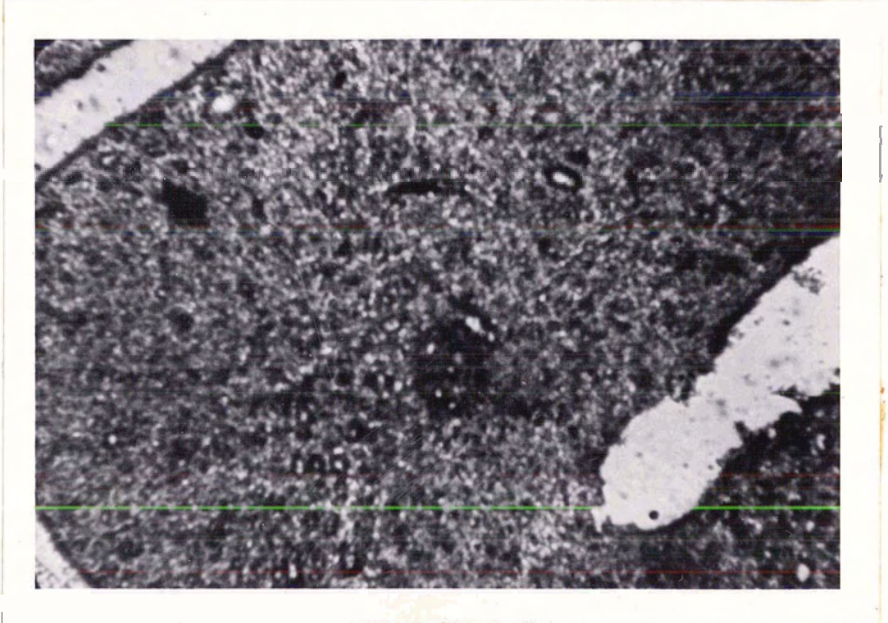
D. Applying acrylic cement

Figure 22

Unstained histological sections



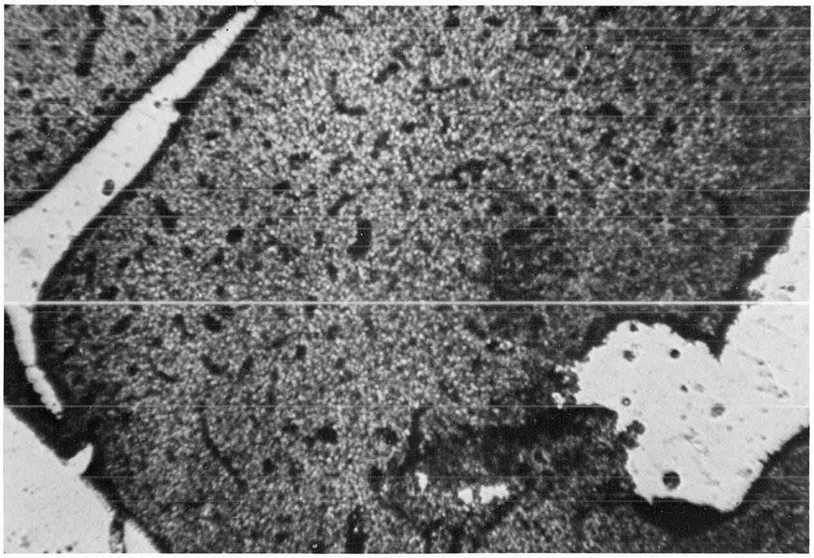
Rat 6



Rat 9

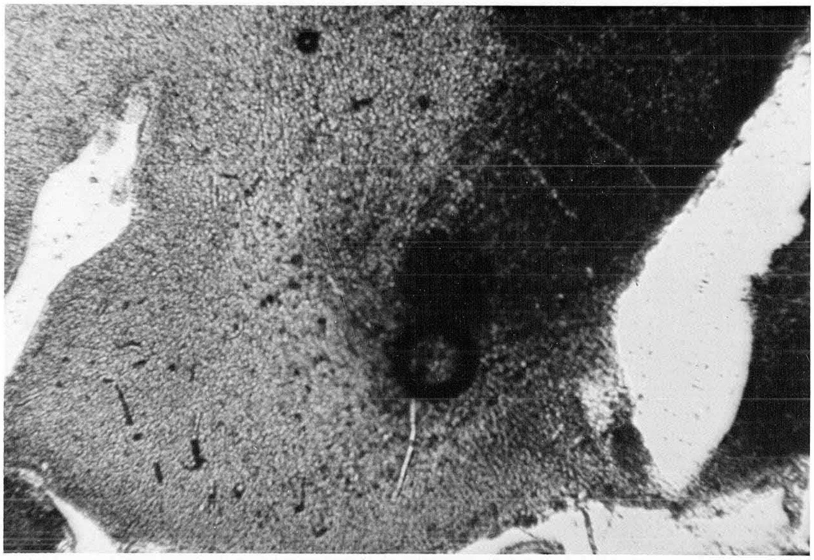
Figure 22 (continued)

third ventricle



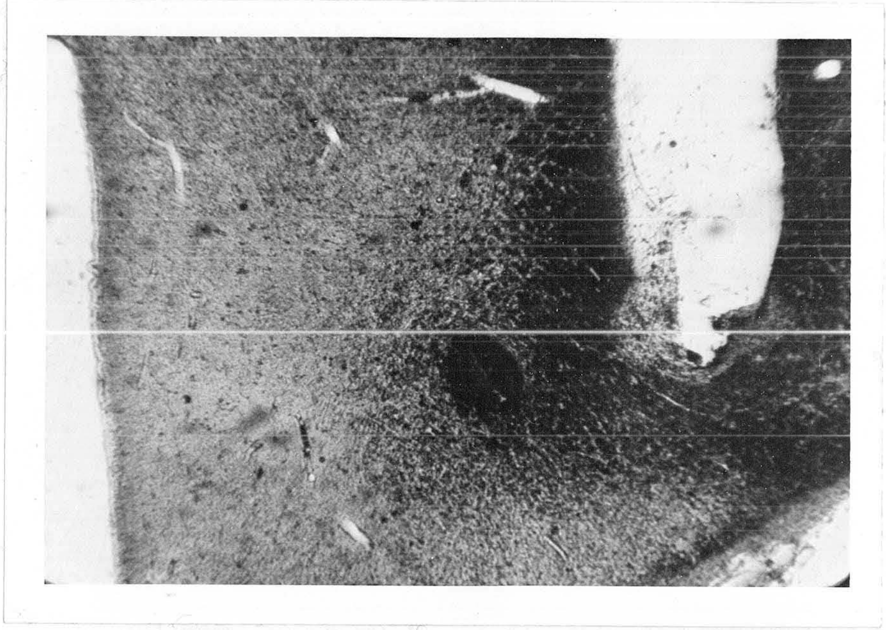
ventral Rat 8

third ventricle



ventral Rat 39

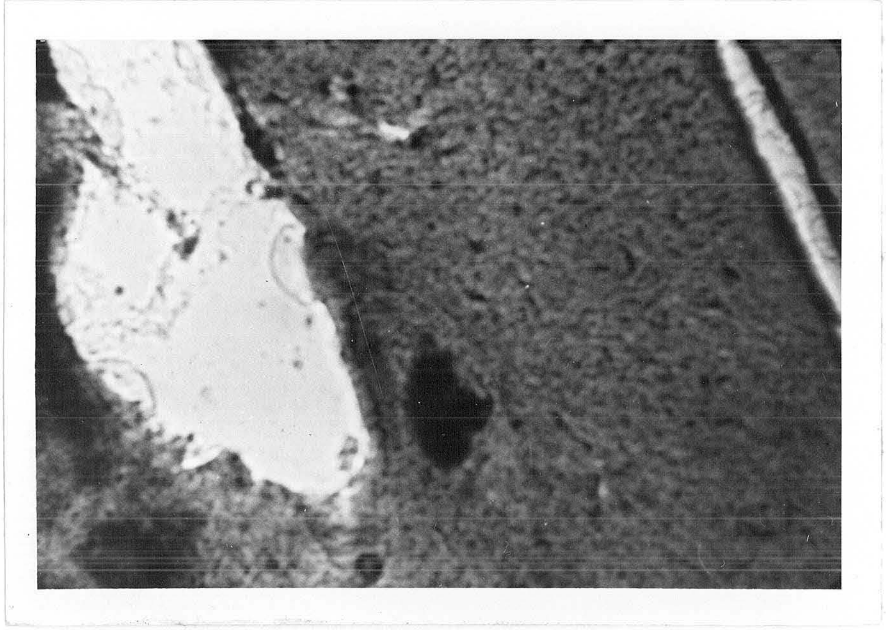
Figure 22 (continued)



third
ventricle

ventral

Rat 26



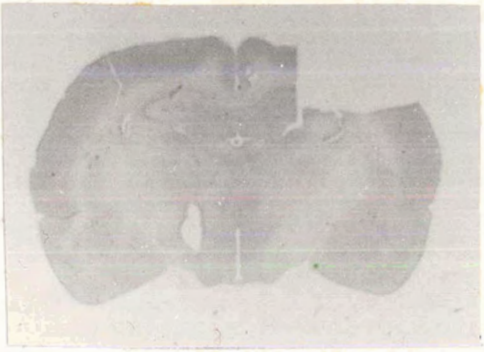
third
ventricle

Rat 3

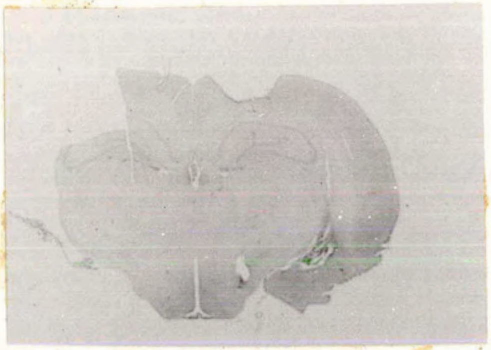
ventral

Figure 23

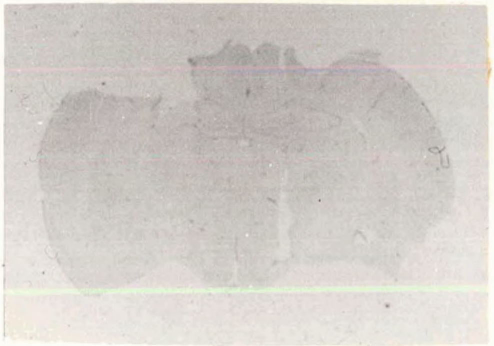
Stained histological sections



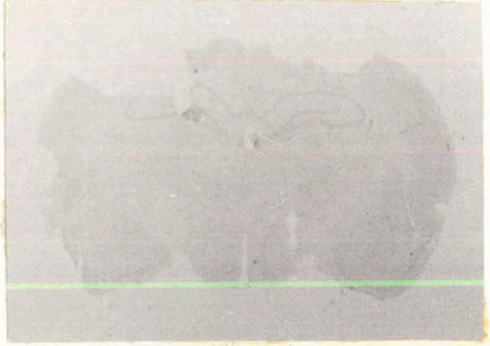
Rat 6



Rat 8

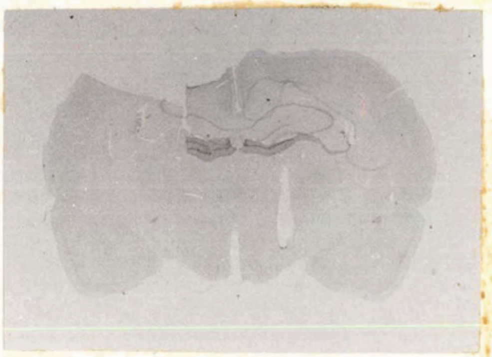


Rat 9



Rat 21

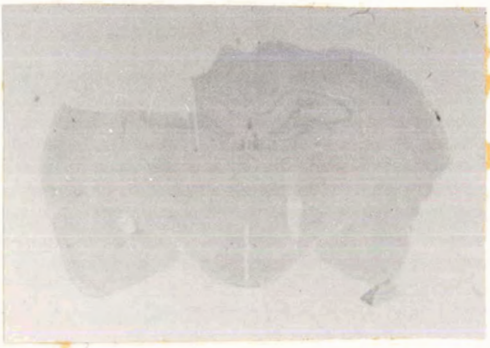
Rat 26



Rat 39

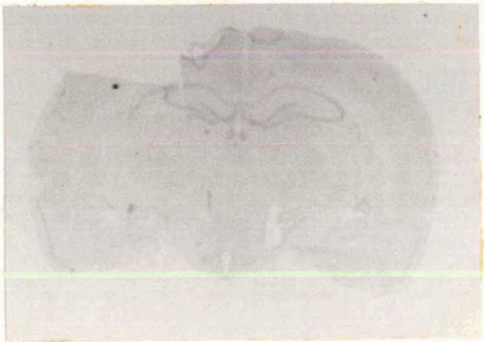
Figure 23 (continued)

Rat 45



Rat 48

Rat 55



Rat 57

Rat 59