

An Investigation of Responding on Schedules of Electrical Brain-Stimulation Reinforcement

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ABSTRACT

In Experiment I, the lever-pressing responses of rats were maintained by reinforcement consisting of single trains of electrical stimulation of the brain (ESB) presented on random-interval (RI) schedules ranging in value from RI 3-min to RI 10-min. Both the cumulative response patterns and the relationship of response rates to reinforcement density were similar to those observed for rats reinforced conventionally. In Experiment II, lever-pressing was reinforced with single trains of signalled ESB, unsignalled response-contiguous ESB, or sweetened condensed milk presented on random-ratio schedules. Most of the ESB-reinforced rats and half of the milk-reinforced rats stopped responding at ratio values exceeding 50:1, while the remaining rats responded at higher ratios. Response rates were higher at lower ratio values for the ESB groups than for the milk group, but as ratio values increased, all groups showed similar decreases in rate. All rats were observed to initiate responding faster than inexperienced control rats and priming was not required.

Ever since electrical stimulation of the brain (ESB) was found to act as a reinforcing stimulus (Olds & Milner, 1954), there has been considerable interest in comparing the behavioural effects of ESB to more natural reinforcers such as food (e.g., see review by Mogenson & Cioe, 1977). The extensive literature on schedules of rein-

forcement (e.g., Ferster & Skinner, 1957) provided a basis for immediate comparisons between these two classes of reinforcing stimuli. Not long after Olds and Milner (1954) reported that continuous reinforcement with ESB could maintain operant responding, Sidman, Brady, Boren, Conrad, and Schulman (1955) found that intermittent schedules of ESB could also maintain behaviour. The latter authors suggested that ESB consisting of one half-second train of pulses may act like small amounts of conventional reinforcement because behaviour was maintained only by low fixed-ratio (FR 7) and short variable-interval (VI 16-sec) schedules. Responding on FR schedules of ESB reinforcement was studied also by Elder, Montgomery, and Rye (1965), Huston (1968), and Keesey and Goldstein (1968); in general, these authors found that, for most animals, responding was not maintained on ratios exceeding 25:1 to 33:1, with very few animals responding at ratios as high as 50:1.

Pliskoff, Wright, and Hawkins (1965) used a different technique of presenting scheduled ESB reinforcement. They trained rats to press one lever to produce extension of a second lever. Each depression of the second lever resulted in a train of ESB and each reinforcement period consisted of from 20 to 100 or more trains. With this technique they observed performance on the first lever on variable and fixed interval and ratio schedules which was similar to performance for conventional reinforcers such as food. Pliskoff et al. (1965) concluded, as did Sidman et al. (1955), that reinforcement consisting of several or many trains of ESB probably should be used to compare schedule performance for ESB and conventional reinforcement.

Previous to the Pliskoff et al. (1965) study, ESB reinforcement was typically pre-

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sented as a single train (usually of half-sec duration), the onset being contiguous with lever depression. This method of presenting reinforcement is unique to ESB. Natural reinforcers studied in the laboratory are delayed for a brief time (e.g., the time it takes an animal to move from a lever to a feeder) after the response occurs. In this regard, natural reinforcement also is signalled insofar as ingestion always follows the actual presentation of the reinforcer. Typical response-contiguous ESB reinforcement is distinctly different since it is not signalled, the presentation of the reinforcer being the only event.

Pliskoff et al. (1965) simultaneously changed both the method of presenting the ESB (by using the two-lever procedure which would provide a signal to the animals indicating the availability of ESB) and the number of trains per reinforcement. In a more recent study, Cantor (1971) varied only the method of presenting the ESB, training rats on interval and ratio schedules with reinforcement consisting of a single train of ESB that was preceded by a brief signal. He observed responding on fixed and variable interval and ratio schedules 'comparable to that typically found with food reinforcement' (Cantor, 1971, p. 612).

Although there have been several reports on the limits of response-contiguous ESB reinforcement density that would maintain FR responding (see above), only the Sidman et al. (1955) study looked at the effects of decreasing response-contiguous ESB density on interval schedule responding. In a recent report, Beninger, Bellisle, and Milner (1977) observed that random-interval schedule responding was maintained equally well by single trains of signalled ESB or response-contiguous ESB. This finding was at variance with the results of Sidman et al. (1955) for interval schedules because responding was maintained on leaner schedules than they reported and questioned the conclusions of Cantor (1971) concerning the role of the signal. The first experiment in the present study

extended this analysis by determining how few single trains of response-contiguous ESB reinforcement would maintain responding on random-interval (RI) schedules. Surprisingly, responding was maintained on RI schedules with an average of only one ESB every 10 minutes for one animal and all animals continued to respond up to or beyond RI 3-min schedules.

The second experiment examined the limits of random-ratio (RR) schedule performance. One group received single trains of ESB which were signalled while the ESB reinforcement was unsignalled and response-contiguous for a second group. To compare the ratio schedule performance of these two ESB groups to a conventionally reinforced group, a third group receiving diluted sweetened condensed milk reinforcement was added. It is important to note, however, that no attempt was made to equate the magnitude of reinforcement of ESB and sweetened milk in these non-deprived rats. The results of this study revealed that with reductions in reinforcement density, all three groups showed considerable overlap in ratio values at which responding ceased.

EXPERIMENT I

The purpose of this experiment was to determine how few single-train response-contiguous ESB reinforcements were necessary to maintain the responding of non-deprived rats on random interval schedules. Millenson (1963) has shown that the behavioural consequences of random-interval schedules are in good agreement with the behavioural effects of variable-interval (VI) schedules.

METHOD

Subjects

Eight experimentally naive male hooded rats of the Long-Evans strain, weighing 350–400 gm at the beginning of the experiment, were individually housed with food and water continuously available.

Surgery and Histology

After anaesthetization with an ip injection of 50 mg/kg Nembutal, each rat was implanted stereotactically with a Plastics Products bipolar electrode (#MS 303-0.010) made of intertwined stainless steel wires .25 mm in diameter. With the incisor bar set at 5.0 mm above the horizontal plane through the interaural line, co-ordinates of 1.6 mm posterior to bregma, 2.0 mm lateral to the midline, and 8.5 mm below the surface of the skull were used with the subthalamic nucleus as the target. Seven days of recovery from surgery preceded the initiation of testing.

Following completion of the experiment, the rats were killed and perfused through the heart with saline followed by 10% formalin. The brains were extracted, fixed in 10% formalin, sliced at 50 μ m, and stained with luxol fast blue followed by cresyl violet to verify electrode loci.

Apparatus

The experimental environment consisted of a Plexiglas cubicle (approx. 22 cm³) with a grid floor and one aluminum plate wall on which was located a lever (Lehigh Valley Electronics model no. 121-03). The lever had a force requirement of .10 N and was 5.5 cm from the side wall, with its surface at a height of 5.0 cm. Eight cm to the right of the lever, at a height of 3.0 cm was an aperture which contained a dipper (Lehigh Valley Electronics model No. 114-02) with a cup capacity of .15 ml. The cubicle was located in a sound attenuating box which was equipped with a speaker providing constant masking noise and a relay which could be used as a 'click' source.

ESB was provided through leads attached to a mercury slipring mounted atop the sound attenuating box, thereby providing the rats freedom of movement. Electrical stimulation consisted of a .5-sec train of biphasic rectangular pulses, each being .1 msec in duration, presented at 100 Hz. The current varied from rat to rat, ranging from 200 to 415 μ A and was kept constant by placing a resistance of 10⁵ ohms in series with the rat.

Solid state switching and timing devices (BRS/LVE) were used to arrange the contingencies. Random intervals were generated by a probability gate (BRS Electronics Model No. PP-1) pulsed by a variable time source with an average pulse frequency of 5 per min; random ratios were arranged, using the same gate fed by responses. Data were recorded on electro-mechanical counters and a timer.

Procedure

Each reinforcement consisted of a .5-sec train of ESB, the onset of which was contiguous with lever depression. In the first session, the lever-press

response was shaped and followed by 10 to 15 minutes of continuous reinforcement (CRF). All subsequent sessions were 30 minutes in duration, occurring at approximately the same time each day five days a week. The schedule in effect during the second session was RI 12 sec, i.e., reinforcement was made available, on the average, every 12 sec. Once it was set up, a reinforcement remained available until it was collected but, if a second was set up before the first was collected, the second reinforcement was lost. All rats received 3 to 5 sessions at this and each subsequent RI value until responding decreased to a rate of less than 1.5 resp/min for 3 consecutive sessions. The series of RI values used began with RI 12 sec, RI 30 sec, RI 45 sec, and RI 60 sec, followed by 30-sec increments up to RI 5 min, then 60-sec increments up to RI 9 min and ending with 3 to 5 sessions, each of RI 9.5 min and RI 10 min for rats that still had not reached the termination criterion.

All rats were trained for 3 additional sessions following the third criterion session. The first of these consisted of 15 to 30 minutes of CRF to reinstate responding, followed by 20 to 30 minutes of responding on the leanest interval schedule that maintained above criterion responding for that individual rat. The subsequent two were extinction sessions of standard 30-min duration. The purpose of the final sessions was to show that the reinforcement contingencies were responsible for maintaining low rates of responding on the leaner interval schedules. Dependent variables were latency to the first response and number of responses per session.

RESULTS

The electrodes for six of the eight rats appeared to terminate in the subthalamic nucleus (STN) as shown in Figure 1B. The electrode tip for Rat 368 was just dorsal to the STN in the H₂ fields of Forel and for Rat 373 was at the border of the ventral STN and the dorso-medial edge of the internal capsule. All placements supported responding reinforced by intermittent ESB; there was no clear relationship between electrode placement and terminal interval value.

The mean response rate (responses per min) for the combined sessions at each interval value that maintained above criterion responding is shown in Figure 2 for all rats. For comparison, Figure 2 also shows the average response rate for 6 pigeons

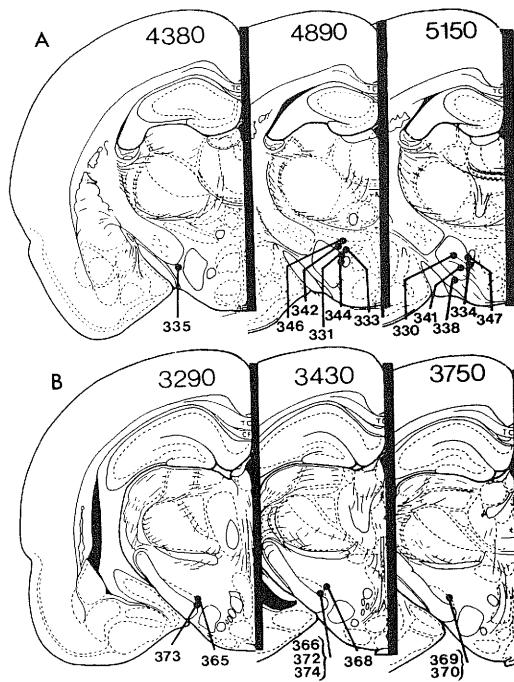


FIGURE 1 Location of electrode tips for the rats of Experiment I (B) and II (A) as plotted on drawings from Konig and Klippel (1963). Numbers on the top of each section indicate the distance in micrometers anterior to the interaural line. Numbers below each section indicate the rat.

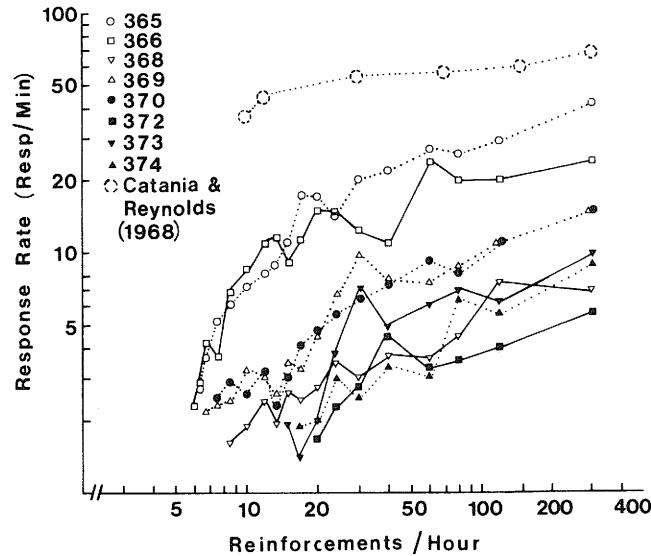


FIGURE 2 Mean response rate for the 3 to 5 sessions at each random interval value (expressed as reinforcements/hour) that maintained above criterion responding in Experiment I. Also shown are data from Catania and Reynolds (1968); each point is the mean response rate for six pigeons at several VI schedule values.

trained on a series of VI schedules from Catania and Reynolds (1968). The data show that rates decreased with decreases in the frequency of reinforcement; in addition the animals that had lower rates when reinforcement density was high tended to reach criterion at higher densities of reinforcement.

Figure 3 shows some representative cumulative response patterns for several interval and extinction sessions. These curves show clearly both continued steady rate responding throughout the interval sessions and negatively accelerated extinction responding.

The other dependent measure was response latency. All of the animals combined had a total of 534 sessions, excluding the initial session of shaping and CRF. In 95% of these sessions the first response occurred within the first 20 sec of the session, and in 50.6% of the total sessions the first response occurred within the first 5 seconds. These latencies do not represent simply the time it took the rats to press the lever accidentally, since five non-reinforced control rats given five 30-min sessions each (see Experiment II

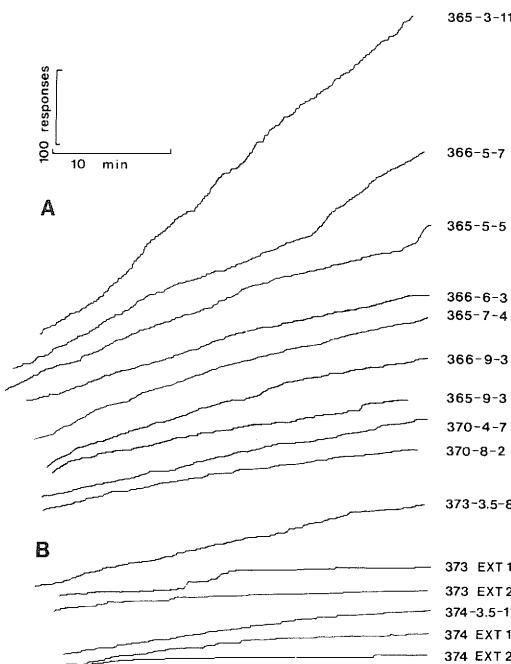


FIGURE 3 Representative cumulative records for rats responding at various RI schedule values in Experiment 1 (A); B is the records from one RI session and two extinction (EXT 1 and EXT 2) sessions for two rats. The three numbers after each record indicate, respectively, the rat, the RI value, and the number of ESBs that were actually delivered during that session.

for details) made a response within the first 20 seconds of a session only 20.0% of the time, and in 44.0% of the sessions never responded within the first 5 minutes.

EXPERIMENT II

The purpose of this experiment was to determine the minimum average ratio of responses to single-train ESB reinforcements that would maintain responding in rats maintained on *ad libitum* food and water. Two ESB groups were included, one receiving unsignalled response-contiguous ESB and the other receiving signalled ESB reinforcement; this was done to determine if there was any difference in ratio performance for ESB presented by these two methods. A third group was trained on progressively leaner random-ratio schedules for diluted sweetened condensed milk

reinforcement to compare performances for ESB and this more conventional reinforcer.

METHOD

Subjects

Nineteen experimentally naive male hooded rats of the Long-Evans strain, weighing 250 to 370 gm at the beginning of the experiment, were individually housed with food and water continuously available, except for 2 days for 6 rats as indicated below.

Surgery and Histology

Thirteen rats were implanted as described in Experiment 1 except that the incisor bar was set at 3.2 mm above the horizontal plane through the interaural line and co-ordinates were .8 mm posterior to bregma, 1.5 mm lateral to the midline, and 8.6 to 8.8 mm below the surface of the skull, with the lateral hypothalamus as the target. Brains were prepared for histology as described in Experiment 1, but were sliced at 40 μ m and stained with thionin.

Apparatus

The environment and control equipment described in Experiment 1 was used.

Procedure

To determine the pre-conditioning value of response latency, five rats with electrodes were each connected to the stimulator and received five 30-min sessions during which no stimulation was given. If no response occurred within the first 5 minutes, the latency was recorded as 5 minutes. Four of these five control rats and the remaining eight naive rats with electrodes were assigned to two groups of six rats each; two of the control (337 and 341) and four naive rats constituted the Signal Group while the other two control (335 and 338) and four naive rats made up the No-Signal Group. The remaining six rats formed the Milk Group.

All rats received one session during which the lever-press response was shaped and followed by a short period of CRF training. For the Signal Group, reinforcement consisted of a train of ESB which was delayed for .5 sec from the time of lever depression and signalled by a click; the onset of ESB was contiguous with lever depression for the No-Signal Group; for the Milk Group, reinforcement consisted of a dipper presentation of .15 ml of Nestle's Sweetened Condensed Milk mixed in 1:1 proportion by volume with water. Rats in the Milk Group were 48-hr

food-deprived before this initial session but were placed back on *ad libitum* food and water immediately following the session and were not deprived for any subsequent sessions. After the preliminary training session, all rats received 2 to 5 sessions at each of a series of random ratio (RR) values until responding was reduced to a criterion level. The RR schedule series was as follows: 1(CRF), 5, 10, 15, 20, 25, 33, 50, 68, 80, 100, 132, 168, and 200. All sessions up to and including RR 132 for Rat 331 and RR 50 for Rat 344 were 30 minutes in duration, while sessions at higher values for these 2 rats were 45 minutes long. The criterion for termination of the series was 3 consecutive sessions with a mean response rate of less than 1.5 per minute. Dependent variables were latency to the first response and number of responses.

RESULTS

Histological data were not obtained for one rat (337) from the Signal Group. Electrodes for the remaining 11 rats were located in the lateral hypothalamic area (LH), lateral (7 rats), ventrolateral (1 rat), dorsolateral (2 rats), or dorsal (1 rat) to the fornix as shown in Figure 1A. According to the atlas of Jacobowitz and Palkovits (1974), all of these placements were in areas containing catecholamine fibres.

The mean response rates (responses per min) for all rats of the 3 groups at each ratio value that maintained rates above criterion are shown in Figure 4. For the Signal Group, all rats failed to respond beyond ratio values ranging from RR 25 to RR 50. The terminal ratio values of the No-Signal Group were significantly more variable, $F(5,5) = 35.5$, $p < .01$, with one rat failing to respond beyond the RR 5 schedule and another continuing up to RR 168. For the Milk Group the variance in ratio values at which responding decreased to criterion rates was also higher than for the Signal Group, $F(5,5) = 77.85$, $p < .01$, and similar to the No-Signal Group, $F(5,5) = 2.19$, $p > .05$, with one rat failing to go beyond RR 5 and another continuing to RR 200. As can be seen in Figure 4C, three rats from the Milk Group continued responding on ratio values greater than 100:1. Since only one of

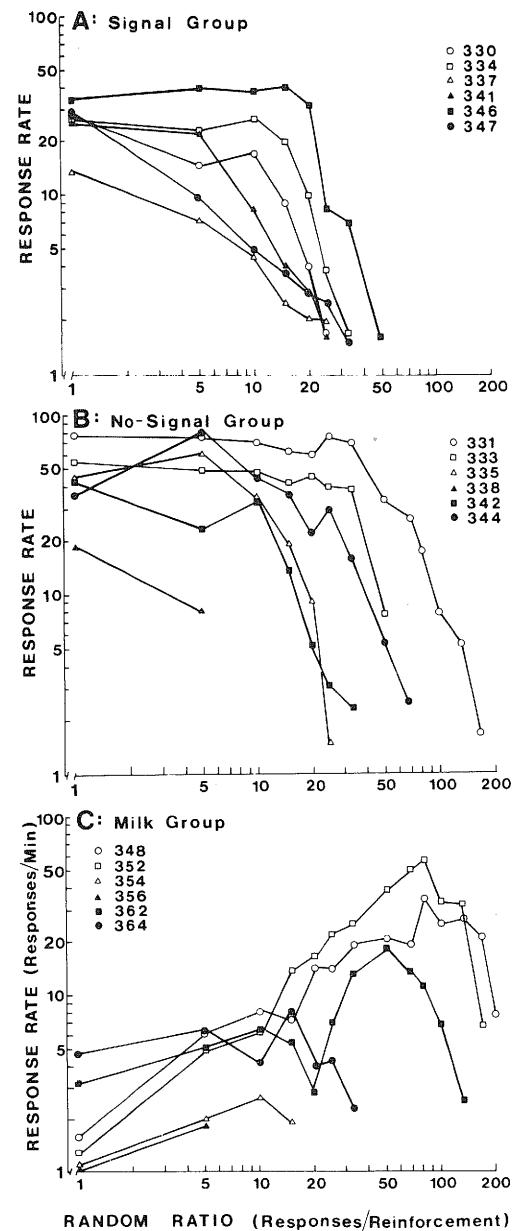


FIGURE 4 Mean response rate for the 2 to 5 sessions at each random ratio value that maintained above criterion responding in Experiment II. The numbers after the symbols in the keys indicate the rat.

the twelve ESB-reinforced rats continued responding beyond RR 100, this would suggest that the milk was a more effective reinforcer than the ESB.

As in Experiment I, the ESB groups generally showed a decrease in response rate

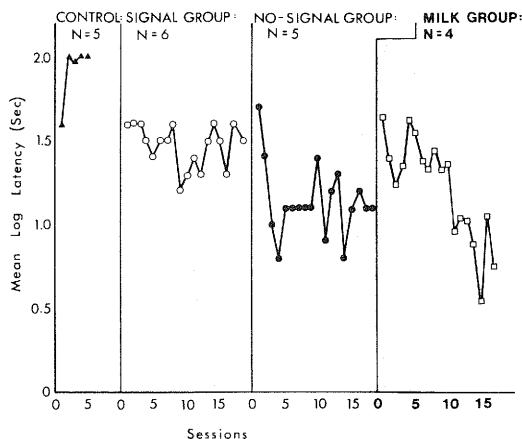


FIGURE 5 Mean log latencies to the first response for the first 18 sessions of each group from Experiment II and the log latencies for five non-reinforced control rats for five sessions.

with decreases in reinforcement density. Rats in the Milk Group, on the other hand, were observed generally to increase response rate with decreases in reinforcement density up to a ratio value usually in about the middle of the range of ratio values for that individual rat; beyond this ratio value rates began to decrease with decreases in reinforcement frequency as they did for the ESB groups. The pattern of responding for all rats was a fairly constant rate throughout the session for ratio values that maintained above criterion rates; as the terminal ratio value was approached for individual rats, responding became more erratic, with pauses interrupting the otherwise constant rate.

With the exception of Rats 338, 354, and 356, all rats in the three groups received at least 18 sessions. Without regard to the ratio values for individual sessions, the logs of latency to the first response for each session were averaged for each group and for five control rats; these means are shown in Figure 5. Log scores were used to meet the requirements of the statistical tests used. By comparing the average log latencies of the control animals to those of the three experimental groups, it is clear that each experimental group consistently initiated responding faster than would be expected by

chance encounters with the lever. A two-way analysis of variance, comparing the three experimental groups, was carried out with groups and blocks of three sessions as the two variables analysed; there was no significant difference among groups, $F(2,12) = 2.552, p > .05$, or across blocks of sessions, $F(5,60) = 1.947, p > .05$. The interaction did not quite reach significance $F(10,60) = 1.830, 0.05 < p < 0.1$; inspection of Figure 5 shows that the Milk Group showed a trend towards shorter latencies across sessions whereas the ESB groups did not, thus accounting for the possible interaction.

GENERAL DISCUSSION

Rats reinforced with ESB on interval schedules (Experiment I) showed cumulative response patterns, at lean reinforcement densities and during extinction, which were comparable to the patterns of behaviour of animals responding for more conventional reinforcers at similar schedule values (Ferster & Skinner, 1957). Furthermore, the relationship of response rate to reinforcement density was similar to that reported by Catania and Reynolds (1968) for pigeons on a more restricted range of interval values as shown in Figure 2. Others have reported that animals will respond for single trains of signalled ESB on VI 2-min schedules (Cantor, 1971) and for reinforcement consisting of multiple trains of ESB (presented on a second lever) on VI 4-min schedules (Pliskoff et al., 1965), but no previous reports have shown a similar maintenance of responding by single trains of response-contiguous ESB reinforcement in rats on *ad libitum* food and water. Using response-contiguous ESB, Sidman et al. (1955) reported that responding in rats was not maintained beyond VI 16-sec; others have reported the maintenance of responding for single trains of response-contiguous ESB on RI 45-sec schedules using rats (Beninger et al., 1977) and on VI 60-sec using (probably food-deprived) rats, cats, and

monkeys (Brady and Conrad, 1960), but these studies were not investigating the leanest density of ESB which would still maintain responding. The poor performance for scheduled ESBs reported by Sidman et al. (1955) may have been related to the septal and caudate placements used.

Of the rats reinforced on ratio schedules of ESB, 10 of 12 ceased responding at ratio values exceeding RR 50, while one rat responded up to RR 68 and another to RR 168. These observations were in good agreement with earlier reports of FR responding; Elder et al. (1965), Huston (1968), and Keesey and Goldstein (1968) all reported that most rats would work on FR 25 or FR 33, with a few going as high as FR 50, and Brodie, Moreno, Malis, and Boren (1960) found that 7 of 8 monkeys ceased to respond for ESB at ratios of 50:1 or less while one monkey continued responding on FR 150. All of these studies used response-contiguous ESB reinforcement and observed comparable ratio performance.

Most studies of ratio schedule performance for ESB have used animals maintained on *ad libitum* food and water. The Milk Group from Experiment II therefore provides a more appropriate comparison for evaluating the similarities of ratio performance for ESB and conventional reinforcement. The observed relationship of response rate to ratio value for the Milk Group was similar to that observed in food-deprived rats trained on FR schedules and in pigeons trained on RR schedules, as discussed by Nevin and Reynolds (1973, pp. 205-207). The ratio values at which the responding of most of the Milk Group ceased were also comparable with those observed by Hodos (1961) and Hodos and Kalman (1963); these authors studied the performance of rats, maintained on *ad libitum* food and water, on progressive ratios using a similar diluted sweetened condensed milk reinforcer, and found that responding ceased at ratios ranging from 40:1 to 160:1.

The observation that some of the rats

reinforced with milk ceased responding at ratio values in the same range as rats reinforced with ESB provides strong evidence that a single train of response-contiguous ESB and a single presentation of a conventional reinforcer have similar effects on the responding of non-deprived rats. It was observed that, generally, with each increase in ratio value, the rates of ESB-reinforced rats decreased whereas the rates of milk-reinforced rats at first increased and then began to decrease. This difference in change in rate may be explained partially by the interference with lever-press responding of consummatory responses for milk; there is no comparable consummatory response for ESB. As ratio values increased for the Milk Group, there were fewer reinforcements presented and therefore less drinking, and sessional rates were observed to increase. With still further increases in ratio value (i.e., greater than 50:1 for most rats), rate reductions were observed in the Milk Group; similar rate reductions were observed in the ESB groups at lower ratios.

The latency data provided clear evidence that animals rapidly initiate responding for ESB at the beginning of a session. This observation is in good agreement with an earlier report (Beninger et al., 1977) and shows that priming, i.e., the delivery by the experimenter of free ESBs at the outset of a session, is not required to instigate responding.

Does signalled ESB have any behavioural effects different from response-contiguous ESB? The only difference between the Signal and No-Signal Group in Experiment II was that the values of the leanest ratios at which responding occurred were more variable for the No-Signal Group, but this may have been related to differences in electrode loci. Beninger et al. (1977) observed that rats receiving signalled ESB on a series of interval schedules showed progressively decreasing response latencies from session to session, whereas rats reinforced with response-contiguous ESB did not; in Experiment II here, however, the two ESB groups

showed no significant difference in the trend of latencies over sessions. From these data it is difficult to conclude that signalled ESB and response-contiguous ESB have any consistently different effects on behaviour.

There are, however, some data which do suggest that signalling ESB may make ESB a more effective reinforcer. For example, Gandelman, Panksepp, and Trowill (1968), Gibson, Reid, Sakai, and Porter (1965), and McIntire and Wright (1965) have shown that extinction responding following signalled ESB training was more vigorous than extinction following response-contiguous ESB. Beninger and Milner (1977) observed that signalling ESB resulted in an attenuation of the intertrial interval effect in the runway. It does, therefore, appear that in some cases providing a signal for each ESB presentation does have an effect on responding. The observation by Steiner, Beer, and Shaffer (1969) that the same rats that would respond for ESBs would escape from the same series of stimulations if it was presented independently of responding also might imply that the effectiveness of ESB as a reinforcing stimulus is not independent of how the ESB is presented.

RÉSUMÉ

Dans une première expérience, le niveau de réponse (presser sur un levier) des rats a été maintenu par un renforcement constitué de salves de stimulations électriques corticales (SEC) présentées selon des intervalles aléatoires (IA) s'échelonnant entre 3 et 10 minutes. Autant l'allure cumulative des réponses que la relation entre le taux de réponse et la densité du renforcement se sont alors avérées semblables à ce qui est trouvé quand le renforcement est conventionnel. Dans une seconde expérience, la réponse (presser sur un levier) a été renforcée soit par des salves de SEC précédées d'un signal, soit par des SEC non précédées d'un signal et faites de façon simultanée avec la réponse, soit enfin par du lait condensé sucré présenté selon des horaires aléatoires. La plupart des rats renforcés par la SEC et la moitié des rats renforcés par du lait ont alors cessé de répondre quand le rapport excédait 50:1, alors que tous les autres rats continuaient de répondre à des rapports plus élevés. Quand les rapports étaient faibles, le

taux de réponse était plus élevé dans le groupe ESB que dans le groupe recevant du lait; mais à mesure que la valeur du rapport augmentait, on observait une diminution semblable du taux de réponse dans tous les groupes. Tous les rats prenaient l'initiative de répondre plus rapidement que des rats contrôles inexpérimentés et n'avaient jamais besoin d'être exhortés à le faire.

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