**CONDITIONED SUPPRESSION OF BEHAVIOR
MAINTAINED BY INTRACRANIAL STIMULATION
AS A FUNCTION OF STIMULATION INTENSITY¹**

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Conditioned suppression was demonstrated in two experiments with rats lever pressing on a fixed-ratio 1 schedule for lateral hypothalamic intracranial stimulation (ICS). In Experiment I, conditioned suppression of responding for low-intensity ICS was obtained with a moderate intensity of foot shock. In Experiment II, low and high intensities of ICS were alternated within the same session and the same animal. The suppression that was exhibited with low-intensity ICS was minimal or absent with high-intensity stimulation, despite the pairing of foot shock with each warning stimulus. Conditioned suppression was a function of ICS intensity, and was independent of response rates. The inverse relationship between ICS intensity and degree of suppression is consistent with a motivational analysis of conditioned suppression. Previous reports of resistance to suppression of behaviors maintained by ICS may now be attributed to the use of high-intensity stimulation.

Although conditioned suppression (Estes and Skinner, 1941) is a reliable conditioning procedure (Blackman, 1972; Davis, 1968; Lyon, 1968), a behavior maintained by intracranial stimulation (ICS) appears to be difficult to suppress (Brady and Conrad, 1960; Merrill, Lott, and Bergen, 1970). Suppression has been reported, but comparison with suppression of behaviors maintained by conventional reinforcers is limited. The reports include two sparsely quantified observations with single subjects (Brady, 1960; Brady and Conrad, 1960), and two experiments in which conditioning was given on one schedule of reinforcement, and extinction on several different schedules (Haworth, 1971; McIntire, 1966). The temporal course of conditioning and extinction of a behavior maintained by ICS has not been presented, and the phenomenon of resistance to suppression remains poorly understood.

The difficulties encountered in previous attempts to demonstrate conditioned suppression may arise from the use of excessive intensities

of ICS. Intensities of 25 mA (peak to peak) (Brady and Conrad, 1960) are incredibly high for reinforcing ICS in the rat; even the range of 30 to 65 μ A (rms) used by Haworth (1971) is more than sufficient to maintain lever pressing. The use of high-intensity stimulation was, in part, a consequence of employing a 60-sec variable-interval reinforcement schedule (Brady and Conrad, 1960; Haworth, 1971), since intermittent ICS schedules require relatively high intensities to maintain responding (Beer, Hodos, and Matthews, 1964; Keesey and Goldstein, 1968). Had responding been reinforced on a fixed-ratio 1 (FR 1) schedule with a moderate intensity of ICS, conditioned suppression of behavior might have been clearly demonstrated. The present first experiment tested this possibility with stimulation of the lateral hypothalamus as the baseline reinforcer.

EXPERIMENT I

METHOD

Subjects

Four naive male hooded rats of the Long Evans strain, obtained from Canadian Breeding Farms, were individually housed in wire cages with food and water continuously available, and maintained on a 15-9 hr light-dark cycle. All rats were handled before use. The body weights ranged between 332 and 397 g at the time of surgery.

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Surgery

Operations were performed under sodium pentobarbital anesthesia (50 mg/kg, i.p.). The bipolar electrodes (Plastic Products Co.) were made of stainless-steel wire (0.25 mm diameter) twisted together, and insulated except for 0.5 mm of the conically ground tips, which were separated by the thickness of the insulation. An electrode was implanted into the lateral hypothalamic area (LH) of each animal (5.4 mm anterior to the interaural line, 1.6 mm lateral to the midline, and 2.5 mm below the horizontal zero plane of De Groot (1959)), and secured to the skull with screws and dental cement.

At the end of the experiment, the animals were anesthetized with sodium pentobarbital and intracardially perfused with physiological saline followed by 10% buffered formalin. After a minimum of two days of fixation in formalin, the brains were frozen-sectioned at 40 μ m and stained with thionin. The positions of the electrode tips were verified with a light microscope. All were in the lateral hypothalamic area.

Apparatus

Testing was conducted in two 19 by 20.5 by 23 cm chambers (LVE No. 1578). A single 18 by 8 mm lever protruded 24 mm from an end panel into each chamber and required a force of 7 g (0.07 N) to trip the attached micro-switch. The lever was mounted 35 mm above the grid floor and 27 mm from a side panel. The Plexiglas sides of the chambers were covered with plastic film, which permitted one-way observation of the animals without disturbing them. Two 8.5-mm diameter speakers were mounted on the Plexiglas cover of each chamber. One speaker emitted the to-be-conditioned stimulus (CS), a 5-kHz, 74-dB tone. The second delivered continuous masking white noise at 60 dB. The sole illumination during training and test sessions was provided by a 6-W jewel light projected through a 13-mm diameter opaque lens 42 mm above the center of the lever. A metal-covered wood block, extending the width of the chamber, was placed under the lever to prevent animals pressing the lever with their electrode assemblies. Counterbalanced electrode leads, suspended from a mercury commutator through an aperture cut in the top of the

chamber, extended complete freedom of movement to the animals.

Brain stimulation consisted of 0.3-sec trains of 0.5-msec rectangular pulses, at a repetition rate of 100 per sec, isolated from the ground. A 470-k Ω resistor was placed in series with the animal to assure relatively constant current. Stimulation intensity was calibrated with a 10-k Ω resistor in lieu of an animal. The unconditioned stimulus (UCS) was a 1.0-mA (rms) scrambled-foot shock of 0.5-sec duration, and delivered through the grid floor of each chamber.

Electromechanical scheduling equipment, housed in a separate room, controlled presentation of the stimuli and recorded responses. Every lever press triggered 0.3-sec duration of brain stimulation irrespective of further responding or holding of the lever. Additional responses made during the stimulation were counted.

Procedure

Animals received a minimum of two days for postoperative recovery. Shaping of lever pressing began with ICS currents between 100 and 120 μ A (peak to peak) and continued with progressive reductions to the lowest value between 40 and 58 μ A that would maintain more than 2200 responses per hour per rat. Animals that did not respond at this rate within this current range were given the least increase in current that would maintain the minimum response rate. Steady responding was attained within five to six 60-min shaping sessions.

Training on conditioned suppression began after responding stabilized. Each daily session (seven per week) was 50 min long, and consisted of four CS presentations, which commenced on the tenth, twenty-second, thirty-fourth, and forty-sixth minutes of the session. There were two days with the CS alone, followed by five days of paired presentations of the CS and UCS, and then 10 days of extinction (CS alone). Each CS continued for 1 min and overlapped with the UCS for 0.5 sec at the end. For each CS presentation, the number of lever presses during the 1 min immediately preceding the CS (A), and the number of lever presses during the CS (B) were recorded, and the suppression ratio (SR) was calculated according to the equation by Annau and Kamin (1961) as follows, $SR = B/(A + B)$.

RESULTS

Conditioned suppression was rapidly learned by all four animals and extinguished slowly (Figure 1). Intensity of the ICS current was progressively increased during training from a mean of 56 to a mean of 69 μ A (Figure 1). The increases were made during the first 5 min of a session, and were used to eliminate pauses in responding, and the tendency to cease responding in anticipation of CS onset. It should not be inferred from the increases that suppression was superimposed upon a weakly supported baseline behavior. Highest individual response rates during the two-CS-only days were 79, 65, 90, and 85 responses per minute, and during conditioning, these had risen to, respectively, 147, 161, 100, and 97 responses per minute (mean pre-CS rates from the fastest sessions). The overall responses of individual animals are summarized in Table 1.

DISCUSSION

The results demonstrate that conditioned suppression of a behavior maintained by an FR 1 schedule of lateral hypothalamic ICS can be obtained with a moderate intensity of foot shock. The acquisition and extinction curves of the suppression of ICS-maintained responding are comparable in form to those reported for conventional reinforcers.

The attenuation of suppression associated with the use of exceedingly high intensities of ICS raises the intriguing conjecture that it is the intensity of the central stimulation that determines the tendency to suppress. Lever pressing for ICS was characterized as being highly

Fig. 1. Suppression ratios and intracranial stimulation (ICS) intensities during the acquisition and extinction of conditioned suppression of behavior maintained by ICS using a foot shock as the unconditioned stimulus (UCS).

resistant to suppression when high-intensity current was used (Brady and Conrad, 1960). In contrast, suppression was readily obtained in the present study with low-intensity ICS. Thus, the appearance or nonappearance of conditioned suppression appears to be a function of the intensity of the ICS current maintaining the baseline. If separate high- and low-intensity ICS conditions were to be presented within the same session to the same animal, would the appearance of conditioned suppression be determined by the ICS intensity? Experiment II was designed to answer this question.

EXPERIMENT II

METHOD

Subjects

Four naive male hooded rats of the Long Evans strain, obtained from Canadian Breeding Farms, were maintained under identical conditions to those of the previous animals, and weighed between 377 and 431 g at surgery.

Table 1

Summary of responses during acquisition and extinction of conditioned suppression of lever pressing for ICS. The means of the daily responses are given for Days 1 to 2 with the CS only, Days 3 to 5 with the CS + UCS, and Days 1 to 3 and 8 to 10 in extinction.

Rat	Days	CS only	CS + UCS			Extinction					
		1-2	1	2	3-5	1-3	4	5	6	7	8-10
150	Pre-CS	150	407	148	378	125	92	292	254	241	586
	CS	239	117	0	0.7	0.3	0	0	0	0	32
151	Pre-CS	208	291	508	515	394	362	355	171	191	340
	CS	240	324	1	1.3	136	333	475	184	244	367
193	Pre-CS	340	390	327	222	204	21	184	244	158	219
	CS	323	86	1	1	32	6	86	324	240	241
194	Pre-CS	256	315	387	230	238	236	241	137	116	52
	CS	270	138	4	3	104	159	161	224	71	32

Surgery and Apparatus

Surgical and histological procedures, and the apparatus, were the same as described in Experiment I. At the conclusion of testing, the electrode placement in each rat was confirmed to be in the lateral hypothalamus.

Procedure

The animals were allowed at least two days for postoperative recovery. Lever pressing for ICS was established on an FR 1 schedule to the same criterion used in Experiment I. Training on conditioned suppression consisted of four CS presentations per 50-min daily session (seven per week), which began on the tenth, twenty-second, thirty-fourth, and forty-sixth minutes of the session. On Day 1, the CS was introduced alone. On Days 2 and 3, the UCS (1 mA, rms, scrambled foot shock) was paired with the terminal 0.5 sec of the CS. Beginning on Day 4, responding was differentially reinforced in the first and second halves of subsequent sessions with either a low or a high intensity of ICS current. The changes of ICS current were gradually made over the 1 min following the second UCS presentation of the session. Thus, on Day 4, lever pressing in the first half of the session was reinforced with the same intensity of ICS that was used for each animal during the preceding three sessions (low current). After the second UCS, the ICS current was increased for all animals to 210 μ A (peak to peak) (high current). On Day 5, the procedure was reversed; high current was made available in the first half of the session and low current in the second half. The daily reversals of the intrasession-ICS-intensity alternations were continued for seven days, and provided four increases from low to high intensity, and three decreases from high to low intensity. Low and high ICS currents were held constant for the individual rats. Small increases were occasionally made during the low ICS current to minimize pauses in responding. The increases were made within 5 min of either the start of a session or following the second UCS. The UCS was applied throughout the intensity alternations.

RESULTS

Acquisition of conditioned suppression was rapid (Figure 2), and suppression and non-suppression alternation was readily attained

Fig. 2. Suppression ratios and intracranial stimulation (ICS) intensities during conditioned suppression of lever pressing maintained by low and high levels of ICS. Responding in the first and second halves of each session was differentially reinforced by either a low or a high intensity of ICS current.

by each animal. The increase in ICS intensity required to produce nonsuppression was nearly three times the suppression intensity (Figure 2). It should be recalled that the UCS was presented with the CS on every alternation trial, including those in which suppression did not occur.

The suppression of lever pressing was independent of the rate of responding. The animals responded at near maximal rates throughout those sessions in which ICS intensity was increased from low to high (Figure 3A). Responding was generally slowed when the ICS intensity was decreased from high to low (Figure 3B). An exception was provided by the rat that responded more rapidly for the low intensity than for the high intensity (Figure 3C). The high rates of responding exhibited by all four animals are evidenced by the representative performances depicted in Figure 3. Total responses and suppression ratios of individual animals are summarized in Table 2.

The animals were clearly affected by the CS in the nonsuppression trials. They paused momentarily at the CS onset (Figure 3), and during the CS they pressed more vigorously on the lever and appeared to be unable to release it smoothly. These small perturbations in their near asymptotic rates of responding are reflected in the consistently depressed SRs ($\bar{X} = 0.43$) on all nonsuppression trials. The animals also reacted to foot shocks at the end of nonsuppression trials with jumps and brief vocalizations.

DISCUSSION

The rapid acquisition of conditioned suppression in this experiment replicates the results of Experiment I. The possibility that

nonsuppression may be attributed to an analgesic property of LH stimulation may be discounted for the following reasons. The rats evinced two separate indications of the undiminished aversiveness of the UCS, reacting to the foot shock with signs of discomfort, and to the CS, which signalled the approaching foot shock, with small perturbations in response rhythms. Moreover, attempts to obtain analgesia with electrical stimulation of the LH of the rat have been negative (Mayer, Wolffe, Akil, Carder, and Liebeskind; 1971).

The intrasession alternation of suppression and nonsuppression indicates that the degree of suppression depends upon the magnitude of a reinforcer as it relates to a given magnitude of UCS. Neither the response rate nor any other feature of the experimental situation appears to control the tendency to suppress. Suppression occurs when a low-value reinforcer is paired with a strong UCS, and the attenuation of the suppression maintained by that UCS can be obtained when the reinforcement is substantially increased. It seems reasonable to postulate that the relationship between the reinforcer and the UCS is reciprocal, that is, suppression and nonsuppression should be obtained by increasing or decreasing the UCS intensity while holding reinforcement intensity constant.

Conditioned suppression was demonstrated in Experiment II to be an extremely flexible phenomenon. This flexibility suggests that the temporal course of the acquisition and extinction of conditioned suppression could be abbreviated or extended simply by increasing or decreasing reinforcer or UCS magnitude, or both concurrently. Both functions might be graphically represented as a family of curves ranging from immediate to protracted learning and extinction.

There are two classes of explanation of conditioned suppression. The first constitutes an analysis at the level of the response and encompasses the competing-response and punishment hypotheses. According to the former, suppression results from the reinforcement by UCS-offset of behaviors that compete with the baseline response. According to the latter, suppression is attributed to the punishment of the reinforced operant by the UCS. The strengths and weaknesses of the response-based explanations of conditioned suppression have been discussed by Lyon (1968).

Fig. 3. Cumulative records showing the intrasession alternation of suppression and nonsuppression obtained as a function of intracranial stimulation (ICS) intensity. Either a low- or a high-intensity ICS was available in separate halves of each session. Downward deflections of the response pen indicate reinforced responses. Downward deflections of the event marker indicate the presence of the 1-min conditioned stimulus (CS). A: increased intensity of ICS current from low to high. B: decreased intensity of ICS current from high to low. C: independence of rate of responding and tendency to suppress, slower responding and nonsuppression during high-intensity ICS, suppression and faster responding during low-intensity ICS.

A second class of explanation proposes a motivational analysis (Estes, 1969; Millenson and de Villiers, 1972). Behavior is considered to be controlled by mutually inhibitory positive and negative motivation systems. Activation of the positive system elicits appetitive and approach behaviors, whereas activation of the negative system elicits withdrawal and defensive behaviors. Conditioned suppression of a reinforced operant results from UCS-activation of the withdrawal system, which, because of the putative property of mutual inhibition, inhibits the appetitive motivation maintaining

Table 2

The total number of responses, and suppression ratios (SR), of rats lever pressing for low- or high-intensity ICS. Two 1-min, pre-CS and CS intervals were presented with each level of ICS intensity.

Day	ICS	Rat 220			Rat 221			Rat 222			Rat 223		
		Pre-CS	CS	SR	Pre-CS	CS	SR	Pre-CS	CS	SR	Pre-CS	CS	SR
4	Low	133	0	0	290	2	.01	175	2	.01	290	2	.01
	High	310	151	.33	222	74	.25	351	314	.47	175	114	.39
5	High	165	147	.47	283	205	.42	302	303	.50	169	80	.32
	Low	70	3	.04	217	24	.10	197	3	.02	291	1	0
6	Low	82	0	0	155	0	0	336	1	0	346	0	0
	High	242	144	.37	273	219	.45	329	262	.44	254	170	.40
7	High	302	217	.42	288	208	.42	284	253	.47	161	114	.42
	Low	49	3	.06	146	2	.01	69	0	0	250	1	0
8	Low	210	5	.02	307	0	0	330	4	.01	279	0	0
	High	266	240	.47	279	213	.43	366	272	.43	198	167	.46
9	High	233	198	.46	268	199	.43	299	261	.47	182	141	.44
	Low	5	0	0	118	0	0	128	0	0	283	1	0
10	Low	9	0	0	229	0	0	240	0	0	292	1	0
	High	129	99	.43	260	221	.46	356	303	.46	189	164	.47

the baseline. Defensive behaviors are then emitted, and in the operant chamber, freezing predominates because fight and escape responses are precluded. Estes (1969) summarized conditioned suppression as a "competition of motives". The intrasession alternation of suppression in Experiment II, obtained by the differential activation of a neural structure intimately involved with appetitively motivated behaviors, strongly supports the motivational analysis of conditioned suppression.

Suppression and resistance to suppression may be restated in terms of the motivational hypothesis as follows. Suppression of an appetitively reinforced behavior occurs when the magnitude of a UCS is sufficient to inhibit the appetitive motivational system of an organism. Contrarily, the absence of suppression, in spite of continued presentations of the CS and UCS, indicates that the UCS is insufficient to overcome the appetitive system. Intermediate degrees of inhibition would be reflected in varying levels of resistance to suppression or incomplete suppression.

REFERENCES

- Annau, Z. and Kamin, L. J. The conditioned emotional response as a function of intensity of the US. *Journal of Comparative and Physiological Psychology*, 1961, **54**, 428-432.
- Beer, B., Hodos, W., and Matthews, T. J. Rate of intracranial self-stimulation as a function of reinforcement magnitude and density. *Psychonomic Science*, 1964, **1**, 321-322.
- Blackman, D. E. Conditioned anxiety and operant behavior. In R. M. Gilbert and J. D. Keehn (Eds.), *Schedule effects: drugs, drinking and aggression*. Toronto: University of Toronto Press, 1972. Pp. 26-49.
- Brady, J. V. Temporal and emotional effects related to intracranial electrical self-stimulation. In E. R. Ramey and D. S. O'Doherty (Eds.), *Electrical studies on the unanesthetized brain*. New York: Hoeber, 1960. Pp. 52-75.
- Brady, J. V. and Conrad, D. G. Some effects of limbic system self-stimulation upon conditioned emotional behavior. *Journal of Comparative and Physiological Psychology*, 1960, **53**, 128-137.
- Davis, H. Conditioned suppression: a survey of the literature. *Psychonomic Monograph Supplements*, 1968, **2**, (14, Whole No. 30).
- De Groot, J. *The rat forebrain in stereotaxic coordinates*. Amsterdam: Noord-Hollandische, 1959.
- Estes, W. K. Outline of a theory of punishment. In B. A. Campbell and R. M. Church (Eds.), *Punishment and aversive behavior*. New York: Appleton-Century-Crofts, 1969. Pp. 57-82.
- Estes, W. K. and Skinner, B. F. Some quantitative properties of anxiety. *Journal of Experimental Psychology*, 1941, **29**, 390-400.
- Haworth, J. T. Conditioned emotional response phenomena and brain stimulation. *British Journal of Psychology*, 1971, **62**, 97-103.
- Keesey, R. E. and Goldstein, M. D. Use of progressive fixed-ratio procedures in the assessment of intracranial reinforcement. *Journal of the Experimental Analysis of Behavior*, 1968, **11**, 293-301.
- Lyon, D. O. Conditioned suppression: operant variables and aversive control. *Psychological Record*, 1968, **18**, 317-338.

- Mayer, D. J., Wolfle, T. L., Akil, H., Carder, B., and Liebeskind J. C. Analgesia from electrical stimulation in the brainstem of the rat. *Science*, 1971, 174, 1351-1354.
- McIntire, W. R. Conditioned suppression of self-stimulation. *Psychonomic Science*, 1966, 5, 273-274.
- Merrill, H. K., Lott, W. J., and Bergen, B. J. Attenuation of a conditioned emotional response via reinforcing intracranial stimulation in rats. *Journal of Comparative and Physiological Psychology*, 1970, 71, 426-434.
- Millenson, J. R. and de Villiers, P. A. Motivational properties of conditioned anxiety. In J. R. Millenson and R. M. Gilbert (Eds.), *Reinforcement: behavioral analyses*. New York: Academic Press, 1972. Pp. 97-128.

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