

Test of Deutsch's Drive-Decay Theory of Rewarding Self-Stimulation of the Brain

Abstract. *Deutsch's theory of intracranial self-stimulation generates experimental predictions regarding the effects of both free stimulation of the brain and the pre-extinction training procedure on extinction behavior after rewarding stimulation of the brain. The results of one experiment confirmed the prediction regarding free stimulation; the other experiment did not provide the expected result. We concluded that Deutsch's theory, in its present form, is of restricted generality.*

While it has been demonstrated that electrical stimulation of the brain (ESB) can serve as a powerful behavioral reward, research has revealed ways in which a response learned for ESB reward differs from topographically similar responses learned for the conventional rewards such as food and water. In order to explain certain of these differences, Deutsch (1) has proposed a theory in which ESB is assigned a double function: it rewards a response which produces it and simultaneously motivates future instances of that response. The disposition or readiness of an animal to engage in behavior maintained by ESB is presumably proportional to the level of this "central motivational state." The relatively fast extinction when a response no longer produces ESB reward is accounted for by postulating a fast decay of the central motivational state after the cessation of stimulation. Howarth and Deutsch (2) tested the prediction that "extinction should be a simple function of time since the last electrical stimulus and would be independent of the number of unreinforced lever presses occurring in that time." Their experimental test of that prediction involved a comparison between two extinction procedures. In the first, they counted the number of responses occurring during normal extinction, that is, with the response lever continuously present, beyond a predetermined number of seconds after the last stimulation. In the second procedure, the lever was withdrawn from the box for the same number of seconds and then reinserted; again the number of extinction responses beyond that point was determined. The data points for the two procedures were virtually identical for each of four different values of time since the last stimulation.

It would seem, therefore, that extinction after ESB reward results from a time-dependent process (inference: decay of the central motivational state) rather than unrewarded responding.

The experiments reported here were designed to test some further implications of that theory. Those implications are:

1) During the period of time that the lever is withdrawn from the box, the application of ESB delivered independently of the animal's behavior should maintain the central motivational state at some appreciable level. When the lever is returned to the box for normal extinction, the animal's output should be greater than if free stimulation were not delivered in the absence of the lever.

2) The results obtained by Howarth and Deutsch in the comparison of the two extinction procedures should be invariant with respect to the details of the lever-training procedure prior to the extinction test, since the decay of the central motivational state is postulated to be a function only of time.

In our first experiment, four rats with chronically implanted, bipolar, stainless-steel electrodes aimed at the region of the posterior hypothalamus were trained to press a lever for ESB reward. Each lever press was rewarded with 100 msec of biphasic, square-wave stimulation, the intensity of which was adjusted for each animal to the minimum value which would produce smooth performance. After several hours on that procedure over a period of days, each rat was exposed to three extinction procedures, the first two of which were similar to those employed by Howarth and Deutsch:

1) The stimulator was turned off and the number of unrewarded responses was determined during the next 22 seconds and in the 10 minutes following.

2) The animals were reconditioned with 2000 rewarded lever presses, after which the lever was withdrawn (3) from the box for 22 seconds. It was then reinserted for normal extinction and the number of responses occurring during the next 10 minutes was determined.

3) Again, the animals were reconditioned with 2000 rewarded lever presses; the lever was then withdrawn from the box for 22 seconds. During those 22 seconds, the animals were given free ESB at the rate of one per second. Each stimulation was identical in all respects to that previously produced by a lever

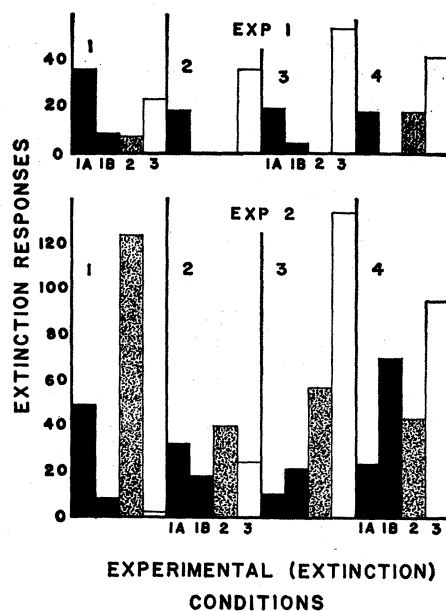


Fig. 1. The upper and lower panels show the number of extinction responses emitted by each animal in the several extinction procedures. The upper panel is for experiment 1, and the lower, experiment 2. See text for explanation of abscissa symbols.

press. After the 22 seconds the lever was reinserted into the box for extinction and the number of responses during the following 10 minutes was determined (4).

The results of this experiment are shown in the upper panel of Fig. 1. The vertical bars show the number of responses emitted by each animal during the three extinction procedures. The bars labeled 1A and 1B are for condition 1 and show respectively the number of responses occurring during the first 22 seconds and the succeeding 10 minutes of normal extinction. Note that for every rat, fewer responses occurred during the 10 minutes of extinction following the initial 22 seconds. The fact that so few responses occurred during the 10-minute period is indicative of the relatively fast extinction often obtained after ESB reinforcement. The mean number of responses for the four rats in condition 1A was compared statistically with the mean number of responses in condition 1B. A *t*-ratio for correlated means of 6.95 (3 degrees of freedom) was obtained, indicating a difference significant beyond the .01 level of confidence. The performance during condition 2 closely approximated that of 1B. That outcome is required by Deutsch's hypothesis and represents essentially a replication of the Howarth and Deutsch findings. While the null hypothesis cannot be

proven, a statistical comparison of condition 1B with condition 2 provided a *t*-ratio for correlated means less than unity. Note the performance in condition 3. For each rat the effect of free ESB during the 22 seconds of lever withdrawal served to increase the number of extinction responses occurring during the 10 minutes following the reinsertion of the lever, as compared with condition 2 where no free ESB was administered. A statistical comparison between conditions 3 and 2 yielded a *t*-ratio for correlated means of 3.93 (3 degrees of freedom), allowing the rejection of the null hypothesis at better than the .05 level of confidence. We may conclude on the basis of this experiment that (i) the Howarth and Deutsch findings are essentially replicable, and (ii) free ESB during the period of lever withdrawal serves to increase the number of unreinforced responses emitted during the immediately succeeding extinction phase. The latter finding is in conformity with expectations from Deutsch's drive-decay hypothesis.

The second experiment, with four fresh rats, was a repetition of the experiment just described in all details except one. During the several days of lever-press training preceding the extinction sessions, the lever was withdrawn from the box every 5 minutes for a period of 22 seconds each time. The lever was then returned to the box and rewarded training continued. At the end of "lever-out, lever-in" training, all four rats in the second experiment displayed a latency between lever insertion and the first rewarded response of less than 1 second. The three types of extinction procedure were run as before and the results are indicated in the lower panel of Fig. 1. A consideration of those data reveal, first, that the neat data relationships among the several extinction procedures in the first experiment have been dramatically changed. In two cases, rats 3 and 4, condition 1B produced more, rather than fewer, responses during extinction. In two cases, rats 1 and 2, free ESB during lever withdrawal served to reduce rather than increase the number of responses emitted during extinction. A second finding from those data is that, in general, overall extinction output and data variability for the four rats is greater than in the first experiment. One statistical comparison was made. The total response output over the three extinction procedures was computed for each of the eight rats. The mean output for the first experiment was compared with the

mean output for the second. The *t*-ratio for uncorrelated means of 4.29 (6 degrees of freedom) is significant at the .01 level. The training procedure, therefore, was a powerful variable in determining extinction performance.

If extinction after ESB reward is understandable solely in terms of a drive-decay process akin to that suggested by Deutsch (1), then the outcome of our second experiment should have been similar to the first. The fact that striking differences were found at tests to the theory's limited predictive value. The data presented by Howarth and Deutsch (2) and in the first experiment described above certainly point to some role played by a time-dependent process. Its exact role, generality, and importance remain to be determined (5).

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References and Notes

1. J. A. Deutsch, *The Structural Basis of Behavior* (Univ. of Chicago Press, Chicago, 1961).
2. C. I. Howarth and J. A. Deutsch, *Science* **137**, 35 (1962).
3. The lever employed in these experiments was a solenoid-operated, retractable lever manufactured by Foringer and Co., Rockville, Md.
4. The actual sequence of the three extinction procedures was varied for the several animals. The results of the first experiment indicated that order effects were unimportant.
5. The experiments reported here were performed under contract No. DA 49-193-2288 between the Office of the Surgeon General, U.S. Army, and the University of Maryland.

20 June 1963

Early Developmental Stress and Later Behavior

Abstract. *The effects of behavioral stress on mice during pregnancy on the behavior of offspring are mimicked by epinephrine injection of mice during pregnancy; hydrocortisone and norepinephrine injection also produce behavioral changes in the offspring. Similar results were obtained in chicks hatched from injected eggs.*

Work by Thompson, Watson, and Charlesworth and by Keeley (1) indicates that severe behavioral and physiological stress to rats and mice during pregnancy (conditioned anxiety, crowding, epinephrine injection) produces permanent changes in the behavior of offspring (changes in open-field activity, defecation, and maze-learning). I here report some preliminary work on the mechanism by which such

changes occur. Injection of stress-syndrome hormones (2) into pregnant mice and into chicken eggs produces changes similar to those produced by subjecting pregnant mice to a behavioral stressor.

In the first experiment, pregnant mice (C57BL/6 strain) (pregnancy determined by the plug method) were divided into five groups: a saline-injected control; an epinephrine-injected group; a norepinephrine-injected group; a hydrocortisone-injected group; a group stressed behaviorally [crowding of females in an 8- by 11- by 5-inch (20.3- by 27.9- by 12.7-cm) cage with ten aggressive males (aggressiveness shown by frequent fights and even killing among the males)]. Treatment was administered during the second trimester of pregnancy; injected groups received four subcutaneous injections on days 8, 10, 12, and 14 of pregnancy. Animals weighed about 21 g, and each injection contained 0.25 μ mole of epinephrine, 0.25 μ mole of norepinephrine, or 2.5 μ mole of hydrocortisone in 0.10 ml of physiological saline solution. Mothers gave birth in individual cages and were not disturbed until 18 days after parturition, at which time cages were cleaned; young were weaned at 30 days. The small numbers of animals prevented cross-fostering.

At 35 days of age, offspring were given individual 10-minute trials in an open-field apparatus [a 20- by 20- by 5-inch (50.8- by 50.8- by 12.7-cm) box ruled off in 2-inch (5.08-cm) squares and illuminated by a 60-watt bulb]. Measurements of locomotion (lines crossed per unit time), defecation, escape jumps (attempts to jump out of the apparatus), and self-grooming activity (a nonnumerical estimate) were made. At 120 days, animals were killed and measurements were taken of brain weight, body weight, and gross brain serotonin and norepinephrine. While the delay is long, measurement at this time is justified by previous experimental findings (1) that the behavioral effects persist to this age.

A summary of the behavioral testing with the appropriate *F*- and *t*-tests is seen in Table 1. The results indicate increased activity and decreased defecation in the offspring of crowded and epinephrine-injected groups when compared to offspring of the saline control, and decreased activity and increased defecation in offspring of the hydrocortisone- and norepinephrine-injected