EFFECTS OF FOOD DEPRIVATION ON FREE-OPERANT AVOIDANCE BEHAVIOR¹

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Lever pressing was maintained by Sidman's shock-postponement procedure and Herrnstein and Hineline's shock-frequency-reduction procedure with rats. Food deprivation to 80% and 70% of the animals' body weights on free feeding resulted in decreased response rates in both avoidance paradigms tested. Reinstatement of free-feeding conditions increased body weights and response rates and decreased shock rates. The effects of food deprivation were not dependent upon any particular avoidance parameters, or types, intensities, or durations of electric shock. These results mean that weight control is essential in long-term studies of avoidance behavior, and in studies of the effects on avoidance behavior of physiological interventions, such as hypothalamic lesions, that themselves may produce weight changes.

Since the advent of Sidman's (1953) free-operant avoidance paradigm, several studies have used this procedure under conditions necessitating food deprivation. One example is the multiple schedule procedure employed by Herrnstein and Brady (1958). During the first stimulus condition, food was presented on a 5-min fixed-interval (FI 5-min) schedule. During the third 5-min stimulus condition, responses initially postponed shock for 20 sec (Sidman avoidance). The second and fourth stimulus conditions were timeout conditions and responses had no scheduled consequences. Another example is the concurrent food-presentation and shock-avoidance procedure (Hearst, 1962; Catania, Deegan, and Cook, 1966). In Hearst's experiment, chain pulling by a rhesus monkey was reinforced on a VI 2-min schedule and lever pressing postponed shock for 10 sec. In the experiment by Catania *et al.*, a press on one lever postponed

shock and a press on a different lever resulted in food presentation on a fixed-ratio schedule.

Both the multiple and the concurrent avoidance-appetitive schedules require food deprivation as a necessary setting condition for the maintenance of behavior by response-dependent food. Since several theoreticians (Hull, 1943; Kendler, 1965) have predicted that food deprivation should affect escape or avoidance behavior, the effect of food deprivation during chronically maintained avoidance behavior requires evaluation.

The literature dealing with food deprivation in shock situations yields three negative results. Food deprivation did not (1) affect shock-detection or shock-aversion thresholds (Misanin and Campbell, 1969), (2) did not modify the probability of shock-elicited activity (Misanin and Campbell, 1969), and (3) did not affect the acquisition of an escape-avoidance response (Amsel, 1950; Dinsmoor, 1958; Misanin and Campbell, 1969). The literature also reveals four positive results. Food deprivation (1) produced greater tolerance to electric shock (Griffiths, 1962), (2) decreased the probability of shock-elicited vocalization (Blanchard and Blanchard, 1966), (3) increased running speed (Amsel, 1950) and decreased response latency (Ley, 1965) during extinction of an avoidance response, and (4) increased shock-escape latencies, resulting in a decrement in the efficiency of escape performance (Meyer, Adams, and Worthen, 1969). The purpose of the present experiments was to assess

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the effects of food deprivation on free-operant avoidance responding maintained by Sidman's (1953) shock-postponement paradigm and Herrnstein and Hinson's (1966) shock-frequency-reduction paradigm.

EXPERIMENT 1: THE EFFECTS OF FOOD DEPRIVATION ON BEHAVIOR MAINTAINED IN RATS BY SHOCK POSTPONEMENT

The purpose of this experiment was to assess the effect of food deprivation on behavior maintained by Sidman's (1953) free-operant shock-postponement procedure. The effect of food deprivation was first assessed with this procedure because it is the most common avoidance procedure in multiple avoidance-appetitive (Herrnstein and Brady, 1958) and concurrent avoidance-appetitive schedules (Catania, *et al.*, 1966; Hearst, 1962).

METHOD

Subjects

Two male hooded rats, CR-3 and CR-4, approximately 1-yr old and 450 g in body weight, were used. Both rats had extensive training (230 hr) on shock-postponement schedules before the start of this experiment. Water was continuously available in each animal's home cage, but unavailable during experimental sessions.

Apparatus

The experimental space was a Lehigh Valley Electronics rat test cage (No. 1417) housed within a sound-attenuating chamber (No. 1417C). A Gerbrand's rat lever requiring 30 g (0.30N) of force to operate was positioned 1.75 in. (4.2 cm) off the floor and 2 in. (5.5 cm) to the left of the center of the stimulus panel. Scrambled shock was delivered by a Lehigh Valley Electronics constant-current dc shocker and scrambler (No. 1531) to the grid floor of stainless steel rods spaced 0.3 in. (1.0 cm) center-to-center. The houselight was on during each session and white noise was supplied to the experimental room to mask the relay equipment in the adjacent room.

Procedure

Sidman's (1953) shock-postponement procedure essentially involves two intervals as basic parameters. In the absence of respond-

ing, there is a fixed time interval (the shock-shock or S-S interval) between the presentation of electric shocks. Each response postpones the impending shock for another fixed time interval (the response-shock or R-S interval).

Experimental sessions were 4 hr long and conducted seven days per week. Feeding conditions were changed after the data were visually inspected and judged not to be varying systematically. During the free-feeding conditions, Purina lab chow was continuously available in the home cage. During the food-deprivation conditions, the animals were fed 5 g of lab chow after the daily session until they reached the desired body weight, at which time the daily ration was adjusted to maintain that weight.

Phase 1. The rats had an extensive history (230 hr) with R-S = S-S intervals of 20 sec and with shocks of 2.5 mA for an inescapable duration of 0.5 sec. The three experimental conditions for Phase 1 were free feeding, food deprivation to body weights that were approximately 80% of the free-feeding weight (80% free feeding), and then free feeding until body weights recovered to approximately 90% of the free-feeding weight (90% free feeding). Experimental sessions were conducted daily throughout the changes in feeding conditions.

Phase 2. Phase 2 was a systematic replication of Phase 1. The same rats were used, but two of the parameters were changed. The S-S interval was reduced from 20 sec to 10 sec and the shock duration was increased from 0.5 to 0.75 sec. As before, R-S = 20 sec and shock intensity = 2.5 mA. The experimental conditions for Phase 2 were free feeding, 80% free feeding, free feeding again, and 80% free feeding again. Between the first 80% free-feeding condition and the second free-feeding condition, experimental sessions were not conducted for 10 days in order to allow the rats to regain their free-feeding weights.

RESULTS

Phase 1. Figure 1 shows the results for Rats CR-3 and CR-4 during Phase 1. In Figure 1, the horizontal lines indicate the means of the body weights in grams, shock rates, and response rates for the last five sessions at each feeding condition. For both rats, as the food-deprivation condition was initiated, body weights and response rates declined. The Pear-

son product-moment correlation between the daily body weights and daily response rates shown in Figure 1 for Rat CR-3 was $r = 0.518$ ($p < 0.001$). The correlation for CR-4 for the same period was $r = 0.818$ ($p < 0.001$). For both rats, intermediate body weights (90% free feeding) resulted in intermediate response rates.

Fig. 1. Response rates, shock rates, and body weights in grams for Rats CR-3 and CR-4 for each session of Phase 1. The vertical lines indicate when changes in feeding conditions were initiated. The horizontal lines indicate the mean values of the three dependent variables for the last five sessions.

The shock rates for CR-3 roughly followed a pattern opposite to the pattern of response rates. As the body weight and response rate decreased, the shock rate increased with food deprivation to 80% free feeding, and then decreased when the 90% free-feeding condition was initiated. The intermediate body weight

(90% free feeding) resulted in a mean shock rate intermediate between the 1.62 shocks per minute mean at 80% free feeding and the 1.03 shocks per minute mean under the free-feeding condition.

A different pattern of shock rates was exhibited by CR-4 during Phase 1. As food deprivation decreased daily weights and response rates, shock rates also declined. The shock rates at 80% and 90% free feeding were 61% and 56% of the free-feeding shock rates (0.62 shocks per minute). This decrease in both response rates and shock rates indicates that there was a change in the animal's temporal patterning of avoidance responses during food deprivation.

To determine if the reduced response rates resulting from food deprivation were associated with any particular segment of the session, the response rates for each half-hour interval of the 4-hr session were computed for the last five sessions of each feeding condition. Throughout the entire 4-hr sessions, for both animals, the 80% free-feeding response rates were consistently below the free-feeding rates, with the 90% free-feeding rates consistently occupying an intermediate value.

Phase 2. Figure 2 shows the daily weights, shock rates, and response rates for Rats CR-3 and CR-4 in Phase 2, with the reduced S-S interval and increased shock duration. When CR-3 was food deprived for the first time in Phase 2, little decrease in response rate was observed, although shock rates increased. Upon return to free feeding, the response rates were higher and shock rates lower than during the initial exposure to free feeding. The second exposure to 80% free feeding resulted in a more discriminable decrease in response rate, although the shock rate increase was not so marked this time. Since the animals were not run for 10 days between the first 80% free-feeding condition and the second free-feeding condition, Pearson product-moment correlations between daily body weight and response rate were computed separately for Sessions 145 to 171, and 172 to 200. These correlations were $r = 0.210$ (not significant) for Sessions 145 to 171, and $r = 0.640$ ($p < 0.001$) for Sessions 172 to 200.

Rat CR-4 showed a marked decrease in response rates and, in contrast to Phase 1, an increase in shock rates during both exposures to 80% free feeding. The Pearson product-mo-

Fig. 2. Response rates, shock rates, and body weights in grams for rats CR-3 and CR-4 for each session of Phase 2. The vertical lines indicate when changes in feeding conditions were initiated. The horizontal lines indicate the mean values of the three dependent variables for the last five sessions. Sessions were not conducted for 10 days between Sessions 171 and 172 for Rat CR-3 and Sessions 172 and 173 for Rat CR-4.

ment correlation between daily body weight and response rate for Sessions 145 to 172 was $r = 0.929$ ($p < 0.001$) and was $r = 0.661$ ($p < 0.001$) for Sessions 173 to 201. Comparing the means of the last five sessions at each feeding condition shows that under the 80% free-feeding condition, response rates averaged approximately 82% of the free-feeding rates. As in Phase 1, the response rate decreases were not associated with any particular segment of the 4-hr sessions.

DISCUSSION

Food deprivation decreased response rates for CR-3 and CR-4 in both phases of Experiment 1, except that the effect was slight during CR-3's first exposure to deprivation during

Phase 2. Two lines of evidence suggest that CR-3's response rates had not stabilized before the first change from free feeding to the 80% free-feeding condition in Phase 2. One is the fact that during the second exposure to free feeding, much higher response rates were exhibited than during the first exposure. Second is the upward trend in response rates during the last two days of the first free-feeding condition.

EXPERIMENT 2: EFFECTS OF FOOD DEPRIVATION ON BEHAVIOR MAINTAINED IN RATS BY REDUCTION IN SHOCK FREQUENCY

Herrnstein and Hineline (1966) introduced a procedure that demonstrated that a response-dependent reduction in shock frequency was a sufficient condition to generate and maintain lever pressing. With their procedure, responding did not postpone shocks for a specific time; it only reduced the overall frequency of shock. In a later report summarizing this work and comparing it to Sidman's shock-postponement procedure, Herrnstein (1969) concluded that this shock-frequency-reduction paradigm was no less effective than other free-operant avoidance procedures in generating lever pressing in the rat.

Experiment 1 demonstrated that food deprivation decreased the rates of responding maintained by Sidman's (1953) shock-postponement procedure. The purpose of Experiment 2 was to assess the effect of food deprivation on avoidance behavior maintained by the shock-frequency-reduction procedure of Herrnstein and Hineline (1966).

METHOD

Subjects

Two male hooded rats, R-65 and R-66, with an extensive history (110 hr) of avoidance behavior maintained by the shock-frequency-reduction procedure, were used. The animal housing conditions were the same as in Experiment 1.

Apparatus

The apparatus was the same as in Experiment 1 except that the shock was ac delivered from BRS-Foringer shock generating (SG-901) and scrambling (SC-901) units.

Procedure

Herrnstein and Hineline's (1966) shock-frequency-reduction procedure involves two separate distributions of shock delivery. One distribution, the high-probability shock distribution, was in effect as long as the animal failed to depress the lever. A tape puller was stepped every 2 sec, and the pattern of shock was varied randomly but with a specified probability of shock of 0.3 for every 2 sec. Thus, if no responding occurred, the rat received a rectangular distribution of shocks with an average rate of nine per minute. The other distribution, the low-probability shock distribution, was in effect dependent upon a lever response by the rat. The low-probability shock distribution had a shock probability of 0.1 for every 2-sec period. Upon a lever depression, the low-probability shock distribution went into effect until a shock was delivered, at which time the high-probability shock distribution was reinstated.

After consistent responding was achieved under free-feeding conditions, the rats were deprived to 80% free feeding. The deprived weights were reached by total food deprivation for the first week, and then 5 g of food per day until the desired weight was attained. After 80% free feeding, the free-feeding condition was reinstated, and then was followed by deprivation to 70% free feeding. Thus, experimental feeding conditions were free feeding, 80% free feeding, free feeding, 70% free feeding, and free feeding again.

Sessions were 100 min in duration and conducted six days per week. The houselight was on for the entire session and each response produced an audible click from a feedback relay. Shocks were 0.8 mA ac with an inescapable duration of 0.3 sec.

RESULTS

The upper half of Figure 3 presents the results for Rat R-65. The horizontal lines indicate the mean dependent-variable values for the last 10 sessions in each feeding condition. Upon initiation of the 80% free-feeding condition, there was a steady decrease in response rates along with an increase in shock rates. The second free-feeding condition increased response rates and decreased shock rates. Subsequent food deprivation to 70% free feeding and then reinstatement of free-

feeding conditions resulted in similar changes in response rates and shock rates. The response rates during 70% free feeding were lower than the rates during 80% free feeding. Conversely, the shock rates were higher during the 70%

Fig. 3. Response rates, shock rates, and body weights in grams for Rats R-65 and R-66 for each session. The horizontal lines indicate the mean dependent-variable values for the last 10 sessions in each condition. The vertical lines indicate when changes in feeding conditions were initiated.

free-feeding condition than during the 80% free-feeding condition. There was increased variability in both response rates and shock rates during the deprivation conditions. The Pearson product-moment correlation between daily body weights and response rates during Sessions 63 through 160 was $r = 0.540$ ($p < 0.001$).

The lower half of Figure 3 shows the data for Rat R-66. Throughout the entire experiment, R-66 exhibited more variability in response rates than R-65. The first change from free feeding to 80% free feeding did not decrease response rates. Resumption of the free-feeding condition increased response rates compared to the rates exhibited during the 80% free-feeding condition and the first free-feeding condition. Food deprivation to 70% free feeding decreased response rates and then increased rates upon reinstatement of the free-feeding condition. Shock rates for R-66 were maintained at the minimum possible except during deprivation to 70% free feeding. If the first free-feeding condition is ignored, the Pearson product-moment correlation between the daily body weights and response rates for Sessions 74 through 159 was $r = 0.476$ ($p < 0.001$).

DISCUSSION

Experiment 2 demonstrated that the effect of food deprivation found in Experiment 1 with Sidman's shock-postponement procedure was not specific to that procedure or to the use of dc shock as the avoidable event. Extension to Herrnstein and Hineline's (1966) shock-frequency-reduction procedure increases the generality of the effect of food deprivation on avoidance behavior. It also supports Herrnstein's (1969) conclusion that the shock-frequency-reduction procedure contains many functional similarities with Sidman's (1953) shock-postponement procedure.

GENERAL DISCUSSION

Two experiments demonstrated that food deprivation decreases free-operant avoidance response rates. The effect was demonstrated with Herrnstein and Hineline's (1966) shock-frequency-reduction procedure and Sidman's (1953) shock-postponement procedure, and was not dependent on any particular one of the procedures, sets of parameters, or types (ac or

dc) of electric shock that maintained the free-operant avoidance behavior.

Two lines of evidence argue that the effects of food deprivation were not due to severe deprivation bordering on physical incapacitation. First, with food reinforcement schedules, it is common to maintain rats at or below 70% of the free-feeding weight (for instance, note the paper by Herrnstein and Brady (1958) in which the rats were maintained at 60% of their 200-day weights). With hooded rats similar to those used in these experiments, I have used an average running-weight of 300 to 325 g for maintaining relatively invariant schedule performance with food presentation over a 2-yr period. This is 60 to 70% of their weight at 200 days when they were first started and about 50% of the weight they would have attained if allowed free feeding for a year. A second line of evidence is that activity as measured in running wheels is negatively correlated with body weight (Duda and Bolles, 1963; Moskowitz, 1959; Treichler and Collins, 1965; Treichler and Hall, 1962). Activity levels in a running wheel increase monotonically as weights are decreased to 60% free feeding. The activity levels at 60% free feeding are 11 (Moskowitz, 1959) to 14 (Treichler and Hall, 1962) times greater than those exhibited on a free-feeding regimen and these increased activity levels are maintained by chronic food deprivation. It is difficult to conceptualize an animal that runs more as a function of an increasing degree of physical incapacitation.

In the present research, the level of food deprivation was defined in terms of per cent of the organism's free-feeding body weight. This definition was used because it is the most common definition in studies that chronically maintain behavior by response-dependent food presentation. However, all of the research on food deprivation reviewed in the introduction used hours since free access to food to define the level of food deprivation. The one experiment, by Meyer *et al.*, (1969), that found reliable effects of food deprivation on shock-escape behavior, and effects in the same direction as the present ones, used 24 and 48 hr of food deprivation. Calculations from the weight data reported show that 48 hr of food deprivation reduced the average weight to 85% of the free-feeding weight (from 285 to 240 g). These findings of Meyer *et al.*, support the findings of the present experiments—food deprivation

that produces a substantial weight loss decreases response rate under escape-avoidance contingencies. None of the other studies on food deprivation reviewed in the introduction used more than 24 hr of food deprivation. The 24-hr food-deprivation schedule, producing less weight loss than 48 hr, coupled with the inherent variability of behavior in experiments that focus on acquisition of responses perhaps explains why previous experiments have found no significant relation, positive or negative, between food deprivation and escape-avoidance responding (Amsel, 1950; Dinsmoor, 1958; Misanin and Campbell, 1969). Just as in the running wheel experiments where no increase in running was observed until body weights decreased to 90% or 85% of the free-feeding weight (Moskowitz, 1959), no escape-avoidance study showed an effect of food deprivation except those that deprived animals enough to produce a body weight below the 90% free-feeding weight.

The present results have two important implications. The first is that any long-term study of free-operant avoidance behavior will require the monitoring and, if necessary, controlling of the experimental organism's body weight in order to preclude variations in avoidance behavior caused by such extraneous variables.

The second implication is for research utilizing physiological interventions in the hypothalamus and their effects on escape-avoidance behavior. The lateral and ventral-medial areas of the hypothalamus have been shown to be important areas for the initiation, maintenance, and cessation of feeding behavior (see Morgane and Jacobs, 1969, for a thorough review). Intervention in either of these two areas produces marked changes in feeding behavior and body weight. Intervention in these two areas has also been demonstrated to affect shock-avoidance behavior (Grossman, 1966; Harvey and Lints, 1965). Destruction of the ventral-medial areas produces an obese animal and also facilitates avoidance behavior, while destruction of the lateral areas produces an aphagic animal with impaired avoidance performance. The present results suggest that the weights of experimental animals should be controlled during investigations of the influence of the hypothalamus on aversively controlled behavior. Weight control would facilitate the determination of whether the effects

on avoidance of hypothalamic intervention are secondary to changes in feeding behavior and weight, or are more primary effects on physiological mechanisms of aversive control.

The decrease in response rates brought about by food deprivation in this study does not support Hull's (1943) drive summation hypothesis or Kendler's (1965) suggestion that food deprivation lowers sensory thresholds and facilitates avoidance performance. These data also appear to contradict aversion threshold data reported by Paré (1969). He defined the aversion threshold as that intensity of shock that was avoided 75% of the time in a tilt cage. He compared young with old, and male with female rats. The only independent measure that showed a significant relation to the aversion threshold was the body weight of the experimental animal. "Light rats have lower thresholds (Paré, 1969, p. 217)." If light rats are more sensitive to electric shock (avoid shocks of lower intensity) than heavy rats, it would seem that any given intensity of shock would be more aversive for the lighter rats, and hence avoided more rapidly and at a higher rate, than the same intensity for a heavier rat. This reasoning has been used to explain why large wild rats need higher shock intensities to maintain free-operant avoidance behavior than smaller wild rats (Powell, 1971). The present experiments showed that within the same subjects, avoidance response rates are decreased by the animal becoming lighter, and not increased as might be predicted from the above between-subject experiments.

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