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Food Deprivation and Food-Delay Effects on the Development of Adjunctive Drinking[1]

ESMERALDA LAMAS AND RICARDO PELLÓN[2]

Facultad de Psicología, Universidad Nacional de Educación a Distancia, 28040 Madrid, Spain

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LAMAS, E. AND R. PELLÓN. *Food deprivation and food-delay effects on the development of adjunctive drinking.* PHYSIOL BEHAV **61**(2) 153–158, 1997.—Twelve rats were food-deprived to 90% or 70% of their free-feeding weights. Food pellets were then delivered every 60 s (Fixed Time 60-s schedule), and the development of adjunctive drinking was measured by the water consumed and the number of licks. For ''master'' rats, each lick was followed by 10-s delays in food delivery. Yoked control rats received food at the same time as their master rats and independently of their own behavior. At 70% deprivation, both master and control rats developed similar levels of schedule-induced licking, but the master rats drank less water. At 90% deprivation, master animals showed little drinking and licking, but the development of adjunctive drinking was not completely prevented. Drinking by yoked control rats did not differ as a function of deprivation level. In showing that lick-dependent delays in food delivery reduce the asymptotic development of adjunctive drinking as a function of the rats' level of food deprivation, these results support the view that environmental influences on schedule-induced drinking are modulated by motivational factors. *Copyright © 1997 Elsevier Science Inc.*

Adjunctive drinking Acquisition Unsignaled delays Food deprivation Licks Rats

FOOD-DEPRIVED rats that are exposed to an intermittent schedule of food reinforcement drink excessive amounts of water, typically drinking after the delivery of the food pellets (2). The rats do not have to drink to obtain the food reinforcer, and this behavior is referred to as ''schedule-induced polydipsia'' or ''adjunctive drinking.'' The phenomenon of schedule induction has been demonstrated with different animal species and with different behaviors (see reviews 6,14,18,21). Despite much empirical investigation, schedule-induced polydipsia and other patterns of induced or adjunctive behavior remain puzzling.

The most notable feature of schedule-induced polydipsia is that it develops in animals that are not thirsty and with no obvious advantage for the animals, appearing to disturb normal water balances in the body (20). From a behavioral perspective, adjunctive drinking has been reported to be relatively insensitive to its environmental consequences. For example, it has been claimed that lick-dependent delays in food presentation were not effective in preventing the development of schedule-induced drinking (3,10,17). However, more recent studies have shown that lick-dependent delays in food delivery can both reduce already developed schedule-induced drinking and attenuate its acquisition (15,16). These effects of lick-dependent delays depended on whether they were signaled or not. Punishment of established patterns of schedule-induced drinking was more effective with signaled delays (15). However, the development of schedule-induced drinking has been shown to be more sensitive to unsignaled delays (13,16). The effects of lick-dependent delays were also a function of the delay duration, both in experiments on maintenance (8) and on acquisition (11,13) of schedule-induced drinking.

The present experiment was designed to further our understanding of the variables that modulate the effects of unsignaled delays on schedule-induced drinking, specifically by investigating whether or not food deprivation also modulates the effects of unsignaled lick-dependent delays on the development of schedule-induced drinking in rats. Previous studies in our laboratory have shown that body-weight loss increased the resistance of established patterns of schedule-induced drinking to reductions by punishment (12). When rats were reduced to 80% or 90% of their free-feeding weights, the schedule-induced licking was decreased by lick-dependent delays, but the delay contingency was not effective in punishing schedule-induced drinking when the rats were maintained at 70% of their free weights.

Food deprivation is a necessary condition for schedule-induced polydipsia to develop, but the amount of excessive drinking reaches its maximum at about 90% of previous free-feeding weights (9). We, thus, set 2 levels of food deprivation, 90% and 70% of the animals' free-feeding body weights, assuming that licking and drinking would not differ between these 2 treatments in control conditions. However, we expected that the acquisition of schedule-induced drinking in rats receiving lick-dependent de-

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[2]Requests for reprints should be addressed to Ricardo Pellón, Departamento de Psicología Básica I, Facultad de Psicología, Universidad Nacional de Educación a Distancia, Ciudad Universitaria, 28040 Madrid, Spain. E-mail: RPellon@cu.uned.es

lays in food presentation would be affected by the different levels of food deprivation.

METHOD

Subjects

Twelve experimentally naive male Sprague–Dawley rats were used. They were supplied by IFFA-CREDO (Lyon, France), and they were approximately 90 days old and with a mean weight of 433 g (range: 376–455 g) at the start of the experiment. Rats 1 to 6 were gradually reduced to 90% of their initial weights by controlled feeding, and Rats 7 to 12 were gradually reduced to 70% of their free-feeding weights. Each rat was then maintained at the specified weight: it was weighed before its daily experimental session and, at least 15 min after the session, it was given an appropriate supplement to the food it had obtained in the experiment. All rats lived individually in an environmentally controlled room (22°C temperature, 60% relative humidity, and 0800 h/2000 h light/dark cycle), with water continuously available in the home cages.

Apparatus

The experiment was conducted in 6 identical Letica Instruments (Barcelona, Spain) LI-836 standard rodent test chambers, 29 cm long × 24.7 cm wide × 35.5 cm high. Each chamber was contained inside a ventilated sound-attenuating chest, with a small observation window in the left wall. The intelligence panel of the test chamber was aluminium, the right side wall was dark acrylic, and the other two sides and the roof were transparent acrylic. No operant levers were installed. A water bottle was mounted on the outside of the right wall of the chambers, with its spout accessible through a hole 3.2 cm wide × 3.9 cm high situated 20 cm from the front wall and 7 cm above the grid floor. The spout was positioned 2 cm behind the hole, so the rat could lick it, but could not maintain permanent contact with it. Licks at the spout were sensed by a photocell beam situated in the hole 1 to 2 mm from the spout. Two 3-W houselights illuminated the chambers during each experimental session. The ambient noise produced by the ventilation fan was 60 dB, which served as masking noise. A Letica Instruments pellet dispenser was located behind the front panel; it delivered 45-mg pellets of standard rat food (Bio-Serve) to a receptacle in the center of the front wall of the chamber, situated 3.7 cm from the grid floor. The scheduling and recording of experimental events was achieved by a BBC microcomputer (Acorn Computers Ltd) programmed in SPIDER™.

Procedure

When the weight of each rat had stabilized at 90% or 70% of its free-feeding weight, a water-ingestion test was given on 2 sucessive days. Sixty 45-mg food pellets were placed together in a dish in the home cages and the amount of water consumed by each rat in 60 min was measured (massed-food test). This measure provided a baseline against which to assess the degree of any schedule-induced drinking subsequently observed in the experimental sessions, where each rat received intermittently the same number of food pellets as during the water-ingestion test.

The rats were then allocated to 6 pairs matched in terms of their water intake during the test (see Table 1). In each pair, 1 rat was designated randomly as ''master'' and the other as ''yoked'' control. The 2 rats in each pair were allocated to different test chambers and were subsequently tested simultaneously.

TABLE 1

MEAN WATER INTAKE (ml) FOR EACH RAT IN THE 2 MASSED-FOOD TESTS AND IN THE LAST 5 SESSIONS OF THE 2 PHASES OF THE EXPERIMENT

	Mean water intake (ml)		
	Massed food	Delay	No delay
Rat 1 (master)	4.5	6.8	7.4
Rat 2 (control)	4.5	38.6	26.6
Rat 3 (master)	2.5	11.6	22.1
Rat 4 (control)	2.0	37.0	31.0
Rat 5 (master)	8.5	11.8	21.6
Rat 6 (control)	5.5	23.0	19.8
Rat 7 (master)	5.0	18.4	35.6
Rat 8 (control)	5.0	39.4	40.8
Rat 9 (master)	7.0	24.2	33.6
Rat 10 (control)	7.0	38.0	37.4
Rat 11 (master)	4.0	23.2	31.0
Rat 12 (control)	3.5	49.4	45.2

Rats were food deprived to 90% (rats 1 to 6) or 70% (rats 7 to 12) of their initial body weights.

All rats were then exposed to the test chambers for 1 h. Twenty pellets of food had been placed in the food receptacle, but the water bottle was not mounted. The houselights illuminated the chamber and the ventilation fan was on, but no other experimental contingency was programmed.

After this pretraining, the experiment proper began. The water bottles were now filled with 100 ml of fresh tap water and installed immediately before each experimental session, conducted 7 days per week. Each session began with illumination of the houselights and delivery of 1 45-mg pellet of food to the receptacle. The houselight was turned off at the end of each experimental session.

In the first phase of the experiment (Delay), the rats were exposed to 42 sessions. In the absence of licks by a master rat, a single 45-mg pellet of food was delivered at regular 1-min intervals independently of the rat's behavior (an FT 60-s schedule). However, each lick by a master rat initiated a 10-s unsignaled delay in the delivery of the next pellet of food. Each lick by the master rat reset this delay. For the appropriate yoked control animal, pellets of food were presented at the same time as to the master rat. There was no programmed contingency between the licking of the control animals and the delivery of food. The sessions terminated with the completion of the interval following the 60th presentation of food.

The second phase of the experiment (No Delay) consisted of 14 sessions. The licks of the master rats no longer had any programmed consequences. All rats were, thus, exposed to a FT 60-s schedule of food presentation. Each session began with the delivery of a pellet of food and terminated at the end of the interval that followed the delivery of the 60th pellet.

The following measures were recorded for each rat each session: 1. the amount of water (to the nearest ml) removed from the bottle, calculated by substracting the residue from the original 100 ml, there being little evidence of ''spillage'' by the rats; 2. the total number of licks per session, which was converted to a measure of licks per inter-pellet interval. The number of inter-pellet intervals and the session duration were also recorded, which allowed for the calculation of the mean duration of the inter-pellet interval for each pair of rats each session.

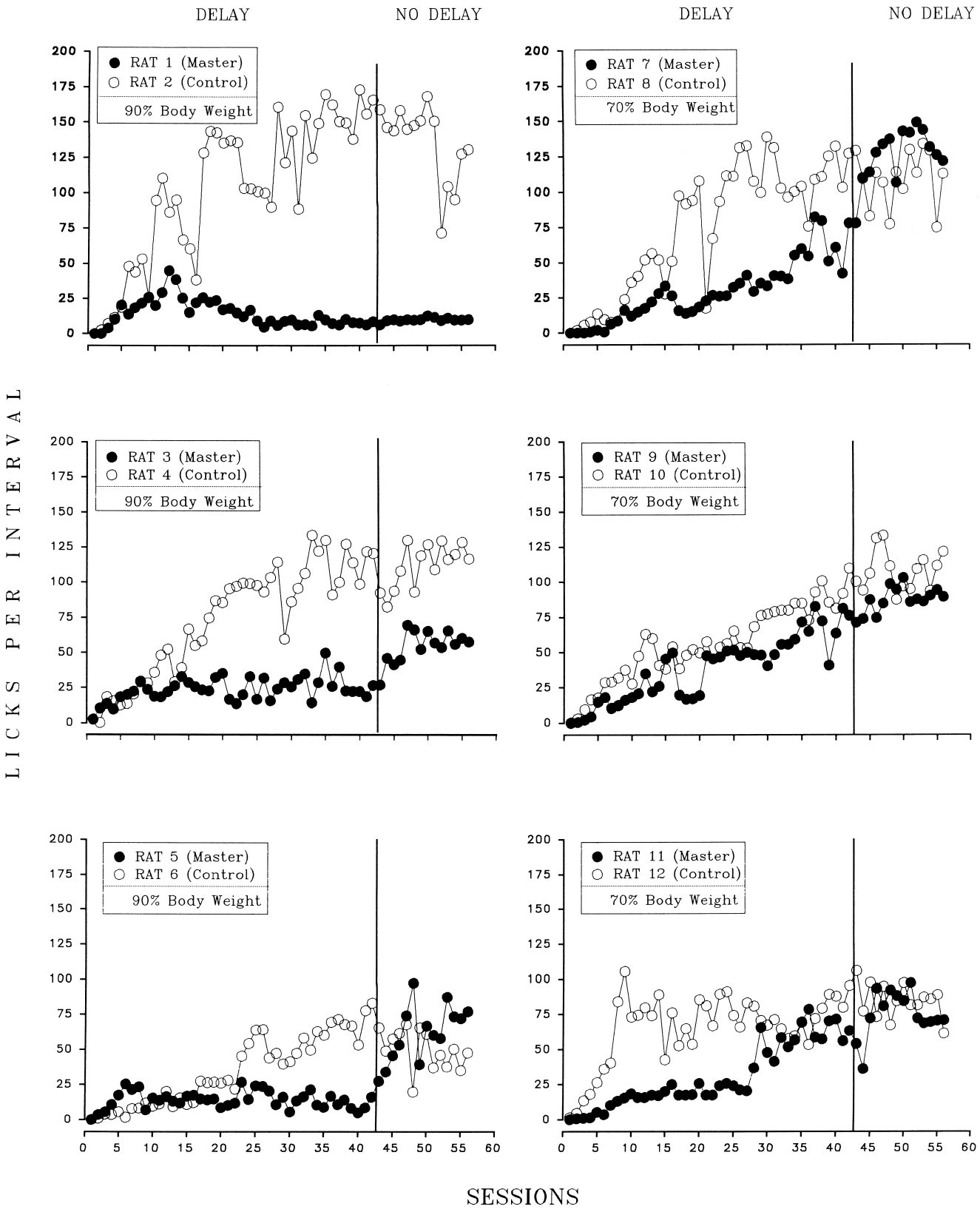

FIG. 1. Daily mean licks per inter-pellet interval for each rat, given as licks per interval (total number of licks divided by 60, the total number of intervals in the session). Each panel depicts the daily data of the entire experiment for a master rat (●) and its yoked control rat (○).

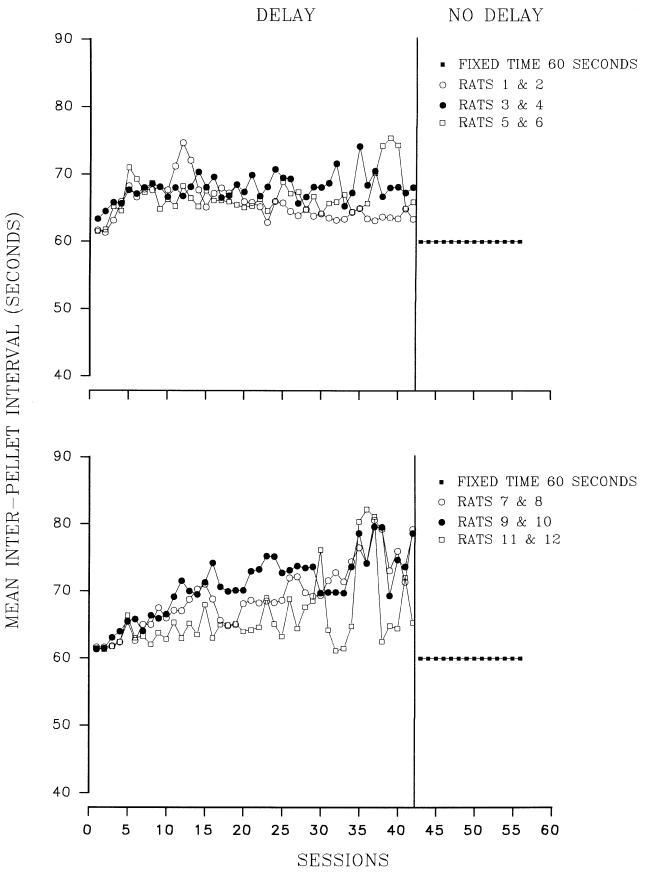

FIG. 2. Daily mean inter-pellet interval for each pair of rats. Rats were food deprived to 90% (upper panel) or 70% (lower panel) of their free-feeding weights.

RESULTS

Table 1 summarizes the mean amount of water drunk by each rat in the 2 massed-food tests and in the last 5 sessions of each stage of the experiment. Within each pair of animals, master and yoked control rats consumed similar small amounts of water during the test, except that Rat 5 consumed more water than its yoked control, Rat 6. At the end of the first phase of the experiment (Delay) all rats drank more than they had in the massed-food test, but the 6 master rats drank less than their respective yoked controls. These differences between master and control animals were most apparent in the pairs of rats submitted to 90% food deprivation (Rats 1-2, 3-4, and 5-6). At the end of the second phase of the experiment (No Delay), all master rats (except Rat 1) showed increases in their water intakes in comparison with those recorded at the end of the first phase, approaching the amount of water consumed by their respective yoked controls. With the yoked controls, and with Master Rat 1, there were no increases in final levels of drinking from the first phase to the second phase of the experiment. All rats, except Master 1, showed drinking at the end of the experiment that can be regarded as excessive or polydipsic (cf. 19).

Figure 1 shows the daily mean number of licks per pellet for each rat. Note that these data are expressed as licks per interval and not as licks per min, because session duration varied as a function of the licking of master rats during the Delay phase. The development of schedule-induced licking can be seen with all 6 yoked control rats in the first phase, reaching levels of licking that were comparable among animals.

The data for the master rats should be analyzed separately, depending on whether they were reduced to 90% or 70% of their free-feeding body weights. Master Rats 1, 3, and 5 (left-hand panels of Fig. 1), which were reduced to 90% of their free weights, never exhibited a large number of licks in the stage with delays, though they initially developed some schedule-induced licking. The greatest licking of Masters 3 and 5 was reached in the earlier sessions (about session 6 to 8), and it continued at about this same level throughout the entire Delay phase. These licks per interval were much lower than those acquired by Yoked Controls 4 and 6, respectively. Master Rat 1 initially developed licking during the first 12 sessions, but this licking subsequently declined to about 10 licks per min. Again, there were large differences in the final amount of licking between Master 1 and Yoked Control 2.

However, Master Rats 7, 9, and 11 (right-hand panels of Fig. 1), whose initial weights were reduced to 70%, developed licking slowly but consistently until approximately session 35. From this session until the end of the Delay phase, the number of licks per interval of these 3 rats stabilized, and it was close to the licks per interval observed for their control animals.

Figure 1 also shows the effects of discontinuing the unsignaled delays (No Delay phase). Five of the master rats (all except Rat 1) showed increases in the number of licks per interval. Most of the yoked controls did not show any increase in this measure. Yoked Control Rat 10 increased slightly the number of licks when the delay contingency was removed, in parallel with the changes observed in the licking of its master, Rat 9. The master rats reduced to 70% of their free-feeding body weights (Rats 7, 9, and 11) reached levels of licking that were comparable to those of their respective yoked controls. Master Rat 5 also did so, but Master 3 did not show sufficient increases to bring the number of licks to the level of its yoked control.

Figure 2 plots the mean daily inter-pellet interval throughout the experiment, calculated by dividing each session duration by the number of food pellets delivered. This interval was, by definition, 60 s in the No Delay phase. With all 6 pairs of rats, the mean interval was close to 60 s at the start of the experiment, reflecting the fact that the master rats had not begun to lick. With Rats 1 and 2 (upper panel), a biphasic pattern is observed in Fig. 2 in the duration of the inter-pellet interval across sessions. The licks emitted by Rat 1 during the early sessions of the experiment (see Fig. 1) caused the inter-pellet interval to rise to 75 s but, when licking was reduced in this animal, the inter-pellet interval decreased to levels approximating 60 s. The inter-pellet interval duration for Rats 3 and 4 (upper panel) showed no sudden changes; however, it tended to increase gradually over the first 8 sessions and then to be sustained at about 68 s throughout the remainder of the Delay phase. The inter-pellet interval duration of Rats 5 and 6 (upper panel) was more variable, and tended to fluctuate around 65 s. In general, the inter-pellet interval in rats submitted to 90% food deprivation rarely exceeded 70 s.

With the pairs of rats submitted to 70% body-weight reduction (lower panels of Fig. 2: Rats 7-8, 9-10, and 11-12), there is a systematic increase in the length of the inter-pellet interval as the sessions progressed, this being a reflection of the master rats increasing their number of licks almost until the end of the Delay phase. This sustained increase was less clear for Rats 11 and 12, which showed much greater variability. The mean inter-pellet interval was close to 80 s for the pairs of rats 7-8 and 9-10 at the end of the Delay phase of the experiment, thus being higher than for the pairs of rats reduced to 90% of their initial weights.

DISCUSSION

The results of this experiment show that 10-s unsignaled lick-dependent delays have an effect on the development of schedule-induced drinking that was dependent on the rats' level of food deprivation. Master rats on a 90% food-deprivation regimen showed final levels of licking and drinking that were much lower than those of their respective yoked controls, and only 2 of these 3 master animals increased drinking when the contingent delays were removed in the final phase of the experiment (this might be due to insensitivity to detect a change in the contingency). On the other hand, master animals on a 70% food-deprivation regimen developed similar schedule-induced licking as their yoked controls when they were exposed to the contingent delays, although this development was not as marked when measured by the amount of water consumed. The differential effect of food delays on master rats at 90% or 70% body-weight reduction is therefore more clearly seen in the measure of licks per interval (Fig. 1) than in the measure of water consumption (Table 1).

Regardless of their levels of food deprivation, yoked control rats did not differ appreciably in their levels of licking and drinking. This is in keeping with previous reports that rates of established schedule-induced drinking do not reflect the degree of food deprivation (5).

It is important to note that most animals subjected to 70% food deprivation (except Rats 11 and 12) received the food pellets at a considerably lower frequency during the Delay phase than during the No Delay phase, when pellets of food were delivered at regular 60-s intervals. This change in the rate of food presentation could explain why all these animals (except Rat 8) increased their licking from the first to the second phase of the experiment (see 4,7), a result that, therefore, is not restricted to master rats. A similar reasoning can be followed to explain why sometimes control animals with 90% deprivation licked slightly more than controls at 70% during the first phase of the experiment, because the former received the food at a shorter interpellet interval (this particularly applies to Rat 2).

The present results, together with those reported by Pellón and Blackman (16) with rats maintained at 85% of their free-feeding weights, support the conclusion that 10-s unsignaled lick-dependent delays reduce the final development of schedule-induced drinking under moderate to intermediate food-deprivation levels (i.e., from 85% to 90%), though they do not completely prevent the acquisition of licking. Thus, all master rats in the present experiment (and in 16) drank more in the phase with delays than they had in the massed-food test. The more severe food deprivation in the present experiment reduced the effects of lick-dependent delays on the development of schedule-induced drinking. The present experiment shows that 10-s unsignaled lick-dependent delays are less effective when rats are more food-deprived.

Similarities between the effects of lick-dependent delays under 85% and 90% food deprivation come also from inspection of how schedule-induced drinking developed across sessions. Rat 1 in the present experiment, maintained at 90% food deprivation, showed some of a biphasic effect of the delay contingency, an increase and then a decrease in the number of licks with sustained training. This effect was also observed by Pellón and Blackman (16) with rats maintained at 85% food deprivation using signaled delays. However, these investigators also reported minor biphasic patterns of responding with unsignaled delays in 2 of their 4 rats. None of the rats maintained at 70% food deprivation in the present experiment showed anything approximating this biphasic effect.

Moran and Rudolph (13) claimed that unsignaled lick-dependent delays of 10 s or 30 s did not reduce the development of schedule-induced drinking in comparison with appropiate yoked control animals (see also 17). Despite some methodological difficulties that may limit the conclusions of Moran and Rudolph (see 16), the present results may in part explain why these authors failed to obtain effects with short lick-dependent delays. The subjects of their experiments (and also of 17) were food-deprived to 80% of their free-feeding weights, a level of food deprivation greater than that used by Pellón and Blackman (16). This may, therefore, lead to results similar to those produced with the 70% deprivation condition used in the present experiment.

The present results amplify our knowledge about the effects of lick-dependent delays on the development of adjunctive drinking in rats. They demonstrate a modulation of the effects of these delays by food deprivation, showing that greater deprivation may interfere with the efficacy of punishment procedures. This same outcome is derived from other studies in our laboratory (12), in which the lick-dependent delays were applied after the normal development of schedule-induced drinking was obtained. Aversive contingencies seem also to be less effective in reducing operant lever pressing as the level of food deprivation is increased (1). Thus, there are further functional similarities between adjunctive and operant patterns of behavior, though, yet again, the present results emphasize the robustness of schedule-induced drinking in rats as a behavioral phenomenon.

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