

COMBINED EFFECTS OF FOOD DEPRIVATION AND FOOD FREQUENCY ON THE AMOUNT
AND TEMPORAL DISTRIBUTION OF SCHEDULE-INDUCED DRINKING

JOSÉ LUIS CASTILLA AND RICARDO PELLÓN

UNIVERSIDAD NACIONAL DE EDUCACIÓN A DISTANCIA, MADRID, SPAIN

Under intermittent food schedules animals develop temporally organized behaviors throughout interfood intervals, with behaviors early in the intervals (interim) normally occurring in excess. Schedule-induced drinking (a prototype of interim, adjunctive behavior) is related to food deprivation and food frequency. This study investigated the interactions that resulted from combining different food-deprivation levels (70%, 80% or 90% free-feeding weights) with different food-occurrence frequencies (15-, 30- or 60-s interfood intervals) in a within-subjects design. Increases in food deprivation and food frequency generally led to increased licking, with greater differences due to food deprivation as interfood intervals became shorter. Distributions of licking were modestly shifted to later in the interfood interval as interfood intervals lengthened, a result that was most marked under 90% food deprivation, which also resulted in flatter distributions. It would therefore appear that food deprivation modulates the licking rate and the distribution of licking in different ways. Effects of food deprivation and food frequency are adequately explained by a theory of adjunctive behavior based on delayed food reinforcement, in contrast to alternative hypotheses.

Key words: food-deprivation level, interfood interval, overall licking rate, temporal distribution of licking, schedule-induced drinking, schedule-induced polydipsia, rats

Schedule-induced polydipsia refers to a behavioral phenomenon that involves the excessive consumption of liquid (normally, though not exclusively, water) as a consequence of intermittent presentation of food pellets for animals that are hungry but not thirsty. One of the most noteworthy features of schedule-induced polydipsia is the postfood location of drinking (Falk, 1961). A burst of licks is normally observed after the consumption of each food pellet, growing to a maximum before the midpoint of the interfood interval and declining gradually thereafter (e.g., Falk, 1966). Staddon and Simmelhag (1971) and Staddon (1977) classified schedule-induced behaviors into two categories according to their temporal location in the interval between biologically relevant events. The first category corresponds to *interim* behaviors, which would be found immediately after the inducing event until midway through

the interval; the second category corresponds to *terminal* behaviors, which would be found at the point at which the interval is drawing to a close and are reminiscent of consummatory behavior. Both interim and terminal behaviors tend to be excessive in frequency. A further category is facultative behavior (Staddon, 1977), which would be characterized by not being excessive and having a temporal location between the above induced interim and terminal behaviors. Under this model, a link can be seen between a behavior's position in the interval and its level of excessiveness, with behaviors observed at the beginning and end of the interval tending to be excessive, and those located between the two not being excessive and, in addition, showing a more flattened temporal distribution. It is safe to say that schedule-induced drinking (polydipsia) is the most widely studied example of schedule-induced interim behavior (for reviews see Pellón, 1990; Reid and Staddon, 1990).

Although the location of schedule-induced drinking is typically postfood, the duration of the interfood interval may also influence the temporal distribution of licks. For instance, in an experiment performed by Segal, Oden, and Deadwyler (1965), in which rats at 80% free-feeding weight were subjected to fixed-time (FT) 30-, 60-, 90-, 240- and 480-s food administration schedules, latency to the onset of drinking increased as the interval between

Research and production of this paper was made possible thanks to Spanish Government research grants PSI2008-03660 (Ministerio de Ciencia e Innovación, Secretaría de Estado de Investigación) and PSI2011-29399 (Ministerio de Economía y Competitividad, Secretaría de Estado de Investigación, Desarrollo e Innovación).

Address correspondence concerning this article to Ricardo Pellón, Departamento de Psicología Básica I, Facultad de Psicología, Universidad Nacional de Educación a Distancia, C/ Juan del Rosal 10, Ciudad Universitaria, 28040-Madrid, Spain (E-mail: rpellon@psi.uned.es)

doi: 10.1002/jeab.53

successive food presentations grew longer (under FT schedules, food is administered at regular time intervals regardless of the animals' behavior). In line with these findings, Rosellini and Burdette (1980), using FT 60-, 120-, 180- and 240-s schedules and recording the lick rate across the intervals in 10-s segments, reported a shift in the peak of drinking toward positions that moved farther away from the time of administration of food as the interval increased. Proportionally, however, the location of the peak was always situated at the beginning of the interval. Shurtleff, Delamater, and Riley (1983) also found that, when rats were exposed to random-time schedules of different durations (10, 20, 60, 120, 180, 300 and 480 s), there was a shift in the distribution of drinking toward positions that were progressively farther from the time of food administration as the mean interval grew longer. Allen and Kenshalo (1976), working with two rhesus monkeys in adjunctive drinking and using fixed-interval (FI) schedules of different durations (1, 4, 8, 16, 32, 64, 128, 192, 256 and 512 s), observed that, while in one of the monkeys the latency between administration of the food pellet and onset of drinking clearly increased in response to a lengthening of the interreinforcer interval, in the other this latency was short (12 to 20 s) and showed no appreciable variation in response to variations in interval duration.

Flores and Pellón (1997) used multiple FI-FT schedules with durations of 15, 30, 60 and 120 s, and measured both the overall rate of licking and the licking rate in 2-s bins across the intervals between food pellets. Regardless of whether the schedule was FT or FI, the temporal distribution of drinking was identical for most interfood intervals (whether or not an operant response for food administration was required seemed to have no clear influence on the temporal location of schedule-induced drinking). Peak distribution was 8 s for the FT and FI 15-s schedules; 10 s for the 30-s schedules; 12 and 14 s for the FI 60-s and FT 60-s schedules, respectively; and 25 s for the 120-s schedules. Relative to the other schedules, at the FT and FI 120-s schedules, Flores and Pellón noted that the distribution was flatter and shifted to the right. Because the ingestion of water at this schedule value was not excessive, the authors postulated that drinking at this schedule value might be a type of adjunctive behavior closer to

the facultative behaviors described by Staddon (1977).

The postfood location of schedule-induced drinking also seems to be influenced by other factors, such as the degree of polydipsic development. Keehn and Stoyanov (1986) used an FI 60-s schedule and recorded the latencies between food and the onset of drinking from the 1st to the 20th training session. They observed that the latency decreased as the number of sessions increased. For example, in the first session the latency was 27 s and 6 ml of water were consumed, whereas in the 20th session the latency to drinking was 6 s and 28 ml were consumed. Schaeffer and Salzberg (1973) subjected rats to an FI 50-s food pellet delivery schedule and analyzed the way in which schedule-induced drinking developed from the start. Initially, drinking behavior was uniformly distributed over time across the interval between food presentations; thereafter, it gradually established itself in the initial portions of the interval and was accompanied by a simultaneous increase in water intake; and, finally, it became located immediately after the ingestion of each food pellet. The results of these experiments suggest that when schedule-induced drinking is not excessive it shows characteristics not typical of interim behaviors (see also Staddon & Ayres, 1975).

Using pigeons and FT schedules, Campagnoni, Lawler and Cohen (1986) investigated the effect of the shift in the distribution of the response peak to a lengthening of the interfood interval. They examined this effect in two different types of behavior: an attack on a representation of another pigeon, which is regarded as schedule-induced interim behavior (Azrin, Hutchinson, & Hake, 1966), and general activity, which, in contrast, is regarded as noninduced behavior (Staddon & Simmelhag, 1971). These researchers observed that the location of the response peak occurred later from the time of administration of the food in the case of the general activity, unlike attack, which displayed the typical postfood location coinciding with the beginning of the interval. In addition, the distribution of general activity proved to be flatter. When the duration of the interfood interval increased, general activity showed a clear shift in the response distribution to the right (i.e., moving away from the time of presentation of the food), whereas for attack the shift was relatively small, giving rise to a

minimum range. These authors concluded that there were two different ways in which the duration of the interval might influence the location of the peak in the distribution of an adjunctive behavior: In one case, an increase in duration would lead to a minimal shift in the peak, and in the other case, the shift would be pronounced. They reasoned that adjunctive behaviors should be divided into two types according to this criterion, depending on how they were affected by changes in the duration of the interfood interval. Schedule-induced interim behaviors are of the first type and non-induced, facultative, behaviors are the second. Furthermore, when this study is viewed in relation to the studies cited above on schedule-induced drinking (Allen & Kenshalo, 1976; Flores & Pellón, 1997; Rosellini & Burdette, 1980; Segal, Oden, & Deadwyler, 1965; Shurtleff, Delamater, & Riley, 1983), they appear compatible in that the latter describe an effect consisting of a more marked distribution shift for long versus short interfood intervals. In short-duration drinking schedules, the pattern would resemble adjunctive behaviors of the first type (i.e., interim behaviors), whereas the adjunctive drinking obtained with long durations between foods would be analogous to general activity in pigeons.

In general, lessening the severity of food deprivation leads to less excessive schedule-induced drinking (Falk, 1969; Freed & Hymowitz, 1972). Falk (1969) reported a drastic reduction in polydipsic levels when animals were left at body weights exceeding 90%-95% of their free-feeding weight. If reducing the level of adjunctive drinking converted this behavior into a noninduced activity, similar to that seen from the above-reviewed literature on food frequency, then satiety would be expected to flatten and shift to the right the peak of the drinking distribution. To characterize this will be one of the purposes of the present investigation.

The amount of schedule-induced drinking is linked to variables that characterize food as a positive reinforcer (for reviews see Pellón, 1992; Reid & Staddon, 1990). Water intake rises in response to an increase in food deprivation or food quantity. Similarly, schedule-induced drinking is related to the frequency of food presentation. While studies have shown the way in which food frequency and amount interact (e.g., Flory, 1971), no systematic studies have been published on either the interactions that

might result from combining different food-deprivation levels with different food-occurrence frequencies, or indeed (as noted above) the specific effects of food deprivation on levels of schedule-induced drinking. These were the general aims of the present study. More specifically, the current experiment sought to examine how a rat's food-deprivation level (reduction in body weight) might affect the shape and location of the peak in the distribution of polydipsic drinking and the effect of the shift in the peak in response to a lengthening of the interfood interval. To this end, we used regimens that generated high rates of schedule-induced drinking, such as FT 15-, 30- and 60-s food schedules (Flores & Pellón, 1997), and subjected the rats to food diets to achieve body weight levels of 70, 80 and 90% of their free-feeding weight, in a within-subjects design whereby all animals were exposed to all experimental conditions at different stages of the study.

This study also indirectly tests the theory that schedule-induced drinking is operant behavior maintained by food reinforcers (see Killeen & Pellón, 2013) with level of schedule-induced drinking expected to be correlated with level of food motivation. According to this theory, the administration of a small amount of food at the end of a temporal interval will sustain a variety of behavioral response patterns, which will follow specific delay-to-food gradients (Pellón & Pérez-Padilla, 2013). In the case of schedule-induced drinking, such food-delay gradients will decay smoothly along the interval, so as to sustain licking at distant temporal locations with respect to upcoming food (i.e., at a postpellet location considering the preceding food). The maximum associability of a response with the reinforcer, and the rate at which the trace decays with increases in the response-reinforcer delay, determines the probability of occurrence of a behavior at specific time points within interfood intervals. In the case of schedule-induced drinking, probability of occurrence will be higher at the beginning than at the end of the intervals because it effectively competes for expression with other behaviors early in the interval, not so at the end of the interval where terminal activities dominate. It is postulated that both the maximum likelihood of association and the rate of trace decay will be changed with variations in food motivation.

Method

Subjects

We used four male Wistar rats that had previously been subjected to schedule-induced drinking procedures with FT 30-, 45- and 60-s food delivery schedules, and were approximately 200 days old at the start of the experiment. The rats were individually housed in home cages in a room with controlled temperature (22°C), relative ambient humidity (60%), and light/dark cycle (8 a.m./8 p.m.). They were subjected to different conditions of body-weight reduction, and were stabilized at 90%, 80% and 70% of their free-feeding weights at the respective conditions of the experiment. The free-feeding weights established just before the start of the experiment were 689 g for Rat 1, 553 g for Rat 2, 660 g for Rat 3, and 529 g for Rat 4, and weight loss was adjusted in accordance with the weight growth curve by age supplied by IFFA CREDDO (Lyon, France). Rats were weighed approximately an hour before the start of experimental sessions.

Apparatus

Four identical 29 × 24.7 × 35.5 cm Letica LI-836 standard rodent-conditioning chambers (Barcelona, Spain) were used, equipped with two levers that were withdrawn throughout the experiment. Each chamber was fitted with a fan; the continuous ambient noise resulting from these ventilation fans was approximately 60 dB and served to mask exterior sound. The front panel of each chamber was aluminum, the right-hand panel was dark Plexiglas, and the left-hand, rear and roof panels were transparent Plexiglas. Each chamber was housed in a dark-walled chest. In addition, each chamber was equipped with a Letica Instruments food-pellet dispenser fitted to the outside of the front panel. The dispenser allowed 45-mg food pellets (BioServ) to be dropped into a hopper, which was accessible to the rat and was mounted in the center of the front panel at a height of 3.7 cm above the chamber floor, a grid consisting of metal bars. The right-hand panel of each chamber was fitted with a device for attaching a water bottle in such a way that the rat could drink from it without difficulty. The spout of this bottle was accessible through a 3.2-cm by 3.9-cm aperture situated 20 cm from the front panel and 7 cm above the grid floor. The spout was positioned 2 cm inside the aperture, so that the

rat could lick it but not maintain permanent contact with it. The licks given by the respective rats to the spout each time they drank water were electronically recorded by means of a closed circuit, to which the 20 parallel stainless steel bars of the grid floor were also connected. The chambers were illuminated during experimental sessions by a 25-W bulb situated on the front wall of the chamber housing, and by two 3-W lamps fitted to the front panel of each chamber. The rats could be observed through a small viewing window. A BBC computer (Acorn Computers Ltd.) programmed in SPIDER was used for scheduling and recording the experimental data.

Procedure

The four rats underwent three different food-deprivation conditions in which free-feeding weights were maintained at 70, 80, or 90%. In each of these conditions, rats were exposed to three different FT schedules: 15, 30 or 60 s. Rat 4 was also exposed to an FT 120-s schedule (see Results for an explanation). One session was completed daily and each consisted of 60 trials (i.e., food presentations); hence, sessions in which, for example, the FT 15-s schedule was administered lasted 15 min. Chambers were checked for food pellets after each session.

Table 1 shows the order in which the conditions were completed and the number of sessions completed at each FT value within a condition. In the first portion of Condition 1, rats completed 45 sessions to ensure that schedule-induced drinking would develop and stabilize in all the rats so as to reduce the effects of their prior experience with schedule-induced drinking. In the first two conditions the FT 30-s schedule was repeated at the end of the condition. The purpose of the reversal was to ensure that the only thing that changed across conditions was the level of food deprivation. The data from these reversals were not analyzed. It should be noted that the order of presentation of the FT 15-s and FT 60-s schedules was balanced across the rats, whether within a given food-deprivation condition (80%) or between deprivation conditions (70% and 90%). The number of sessions completed in each condition was the same across rats and was sufficient to establish stable behavior. Weight adjustments and stabilization between conditions took 25 days, during which training was interrupted.

Table 1
Outline of the procedures followed with each of the rats.

Rat	Condition	Food Dep.	FT	Sessions
1&2	1	80%	30 sec	45
			60 sec	25
			15 sec	25
	2	70%	30 sec	25
			30 sec	20
			15 sec	20
			60 sec	20
			30 sec	20
			30 sec	20
	3	90%	30 sec	20
			60 sec	20
			15 sec	20
3&4	1	80%	30 sec	45
			15 sec	25
			60 sec	25
	2	90%	30 sec	25
			30 sec	20
			15 sec	20
			60 sec	20
			30 sec	20
			30 sec	20
	3	70%	30 sec	20
			60 sec	20
			15 sec	20
4	3	70%	120 sec	20

Data (licks per min and lick counts in 3-s bins) are averaged over the last five sessions completed at each FT value of each condition.

Results

For each rat, Figure 1 shows the amount of adjunctive drinking measured in licks per min on the vertical axis, and the different interfood interval durations under the respective FT schedules on the horizontal axis. Positive linear functions generally related licks per min to food frequency, with higher licking normally occurring at shorter FT values. Only Rat 4, at 70% food deprivation showed a clear bitonic (as opposed to linear) function with maximum licks per min under the FT 60-s schedule, which was why this animal was further tested under the FT 120-s schedule. At 90% free-feeding weight, Rat 3, and possibly Rat 1, displayed something approximating a bitonic function. All rats in all conditions collected and ate all of the food pellets delivered.

Increases in food deprivation generally led to an elevation in licking rates. Licks per min were

higher under 70% food deprivation than under 80% body-weight reduction, and both were substantially higher than under the 90% regimen. This was true for Rats 1 and 3 under the FT 15-s schedule, and Rats 1, 3, and 4 under the FT 30-s schedule. The same pattern of results was observed for Rat 4 under the FT 60-s schedule. While Rat 2's licking displayed no difference between the 70% and 80% food-deprivation regimes at any food frequency, it was significantly higher than under the 90% deprivation condition. Rat 4 registered more licks in the 80% than in the 70% condition under the FT 15-s schedule (a trend that was likewise observed for Rat 2).

Figures 2, 3 and 4 depict the temporal distributions of licks for each rat at the different deprivation levels and under the FT 15-, 30-, and 60-s schedules, respectively. The interfood intervals, divided into 3-s bins, are shown on the horizontal axes, and the percentages of licks in each bin are shown on the vertical axes (the data from which these percentages were drawn are listed in Appendices 1, 2 and 3, corresponding to the FT 15-, 30-, and 60-s schedules, respectively). As can be seen for the different interval durations and food-deprivation levels, in general a similar trend was found, with licks increasing from the beginning of the interval, reaching a peak, and gradually decreasing thereafter. Increased levels of food deprivation, particularly between the 70% and 90% conditions, tended to produce leftward shifts in either the distribution or the peak of the distribution of licks within the interfood intervals. This leftward shift occurred even in cases where food deprivation did not affect the overall amount of licking (such as under the FT 60-s schedule in most rats). Exceptions to this rule were Rat 4 under the FT 30-s schedule and, to a lesser extent, Rat 2 under the FT 15-s schedule. Under these schedules, the rats showed more shifts to the left under the 80% food-deprivation regimen. In other cases, the 70% and 80% conditions resulted in similar distributions of licking, such as Rat 2 under the FT 30- and 60-s schedules, and Rats 3 and 4 under the FT 15-s schedule. Under 90% food deprivation, distributions generally tended to be flatter and shifted to the right (peaking at longer interfood intervals). Changes in the temporal distribution of licking depended on FT length, with more orderly shifts as food-presentation frequency decreased.

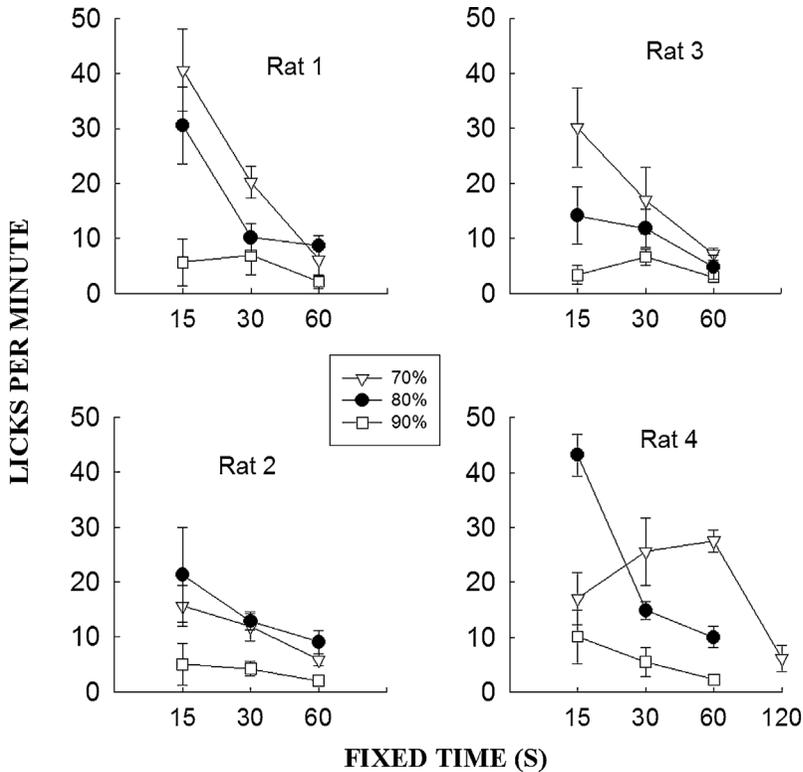


Fig. 1. Individual graphs for each rat, depicting the function defined by the number of licks per minute and the duration of the interfood interval (determined by the values of the FT 15-, 30-, 60- and 120-s) for each of the three food deprivation levels (70%, 80%, and 90%). Data based on the mean drinking rates over the last five sessions of each experimental stage.

Discussion

The aims of this study were to ascertain how level of food deprivation might affect the distribution of schedule-induced licking, the effect on such distribution of lengthening the interfood interval, and to relate these effects to molar rates of licking. In general, the results show that, at the lowest deprivation level (90%), the peak in the distribution tended to be situated to the right vis-à-vis the other deprivation levels but that this effect was more marked at longer interfood intervals. Furthermore, distributions tended to be flatter for the lowest deprivation level, and the molar data (i.e., licks per min averaged over the session) systematically reflected lower drinking rates for this versus the other deprivation levels. We will address the molar, and then the molecular results.

It is interesting to recall here that, when Falk first reported schedule-induced polydipsia, a number of hypotheses were soon proposed to

account for it. Stein (1964) suggested that it could be prandial drinking, with water simply being drunk after the ingestion of solid dry food, such as a food pellet. Intermittent delivery of the dry food would lead to the water consumption after ingestion of each food pellet. However, Falk (1967) showed that schedule-induced polydipsia also occurs after ingesting liquid food. The results of our experiment offer further evidence against this theory because drinking rates for the 90% deprivation level were lower—and in some instances, remarkably so—than those for the 80% and 70% deprivation levels (see Fig. 1) despite the fact that the same number of pellets were delivered in all sessions and the rats consumed all the pellets administered in each session. The fact that drinking differs according to the specific food-deprivation level cannot be explained by the prandial-drinking hypothesis.

Similarly, the current results cannot be explained by any effect of water deprivation

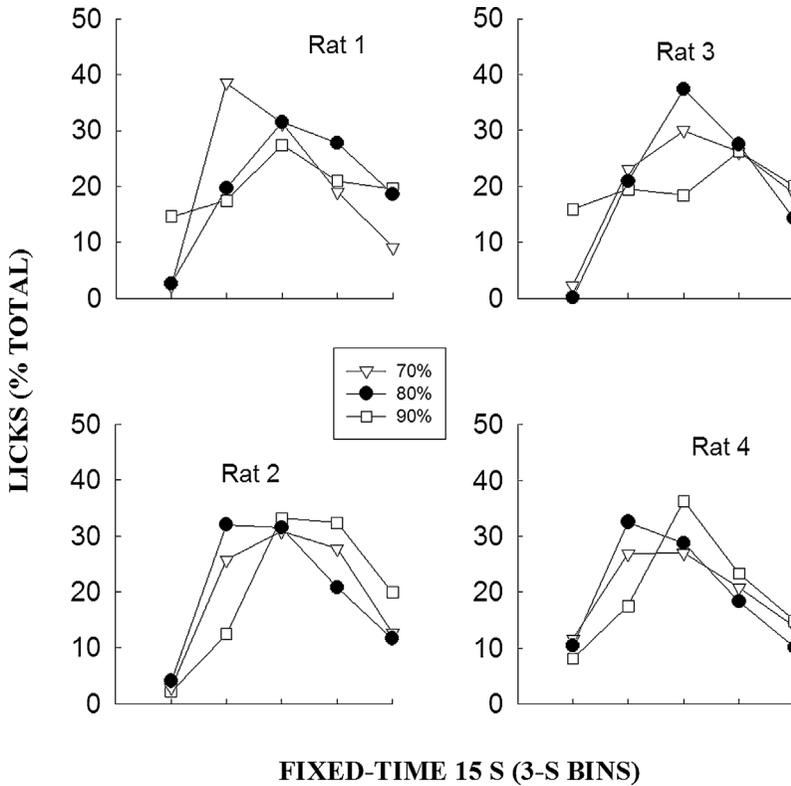


Fig. 2. Individual graphs for each rat under the FT 15-s schedule for licks at each of the different deprivation levels (70%, 80%, and 90%) across the 3-s bins of the interfood interval. The vertical axis represents the percentage of licks given per bin over total licks in the interfood interval. The values of the points are the mean licks over the last five sessions of the respective experimental stages.

(Stricker and Adair, 1966). Whereas rats with a higher level of food deprivation normally ingest (non-schedule-induced drinking) a smaller quantity of water (Bolles, 1961), in our study it was the condition with the greatest degree of food deprivation that developed the highest level of adjunctive drinking.

If the rats' drinking is not due to prandial thirst or need of water, why then do they drink? It has been suggested that the postreinforcement periods are aversive, and that the animals might drink to escape from this aversive situation. Escape responses of this kind would be adjunctive behaviors (Palya, 1993). In situations of greater weight reduction, administration of food would be more reinforcing, and postfood periods would, by extension, be more aversive. Consequently, higher levels of adjunctive behavior would accompany such conditions of greater deprivation. In line with this explanation, we observed that the rats developed a

greater amount of polydipsic drinking at the 70% and 80% than at the 90% weight-reduction levels. However, we also observed that in general more licking was induced at shorter FT schedules, and this is contrary to what would be expected from the aversive interpretation, according to which the less frequent reinforcement the more aversive the schedule should be, hence sustaining more escape responses (licks). The same criticism is valid for Staddon's (1977) motivational model of adjunctive behavior described in the first paragraph of the Introduction, in which interim activities are induced at periods of low reinforcement probability, thus predicting more licking at longer interfood intervals.

As an alternative to the explanation of aversiveness (based on a process of negative reinforcement), it is better to consider that food is acting as a positive delayed reinforcer for drinking (Killeen & Pellón, 2013). This positive

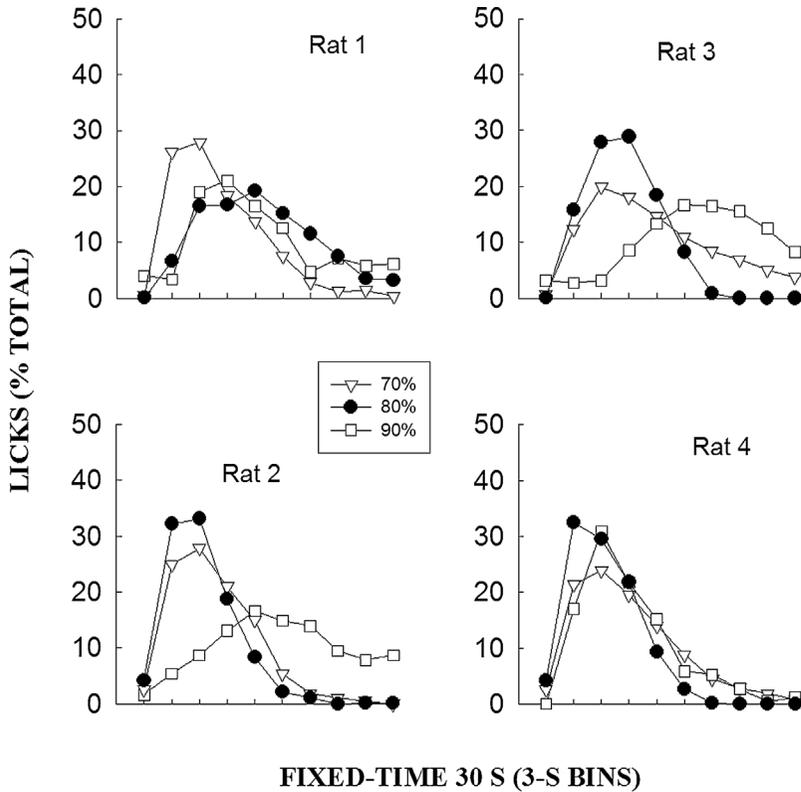


Fig. 3. Individual graphs for each rat under the FT 30-s schedule for licks at each of the different deprivation levels (70%, 80%, and 90%) across the 3-s bins of the interfood interval. The vertical axis represents the percentage of licks given per bin over total licks in the interfood interval. The values of the points are the mean licks over the last five sessions of the respective experimental stages.

reinforcement theory of adjunctive behavior not only explains the greater amount of drinking induced by larger food deprivation (see below)—as does the aversive theory—but also accounts for the greater amount of drinking obtained with shorter interfood intervals. As behavior is closer in time to next food delivery the greater the strength of that behavior should be (Killeen & Pellón). Because animals tended to concentrate licking early in interfood intervals (see Figs. 2, 3 and 4), they experienced a longer interval between the end of licking and the occurrence of food as the intervals grew longer (from 15 to 60 s). This could explain the generally lower rate of licking as food frequency decreased. Under the FT 15-s schedule, animals might not have enough time to perform the entire drinking pattern because the occurrence of food truncated its normal occurrence, but if this was the case it would favor the argument presented here that the shorter the interfood

interval, the higher the rate of responding (see below for further discussion on within-trial distribution).

As for the effect of body-weight reduction, the reinforcement theory of adjunctive behavior suggests that as food deprivation increases the associability of licking and food increases, such that food delivery is more likely to increase the probability of drinking relative to lower levels of food deprivation. This general account of food-deprivation effects should be complemented by the assumption that the different levels of food deprivation will sustain different rates of trace decay, so as to explain that differences due to food deprivation were most evident at short rather than long interfood intervals (see Fig. 1, from FT 15 to 60 s).

The molar data indicate that the greater the weight loss, the greater the amount of adjunctive drinking. Earlier studies support this relationship (Falk, 1969; Freed & Hymowitz, 1972),

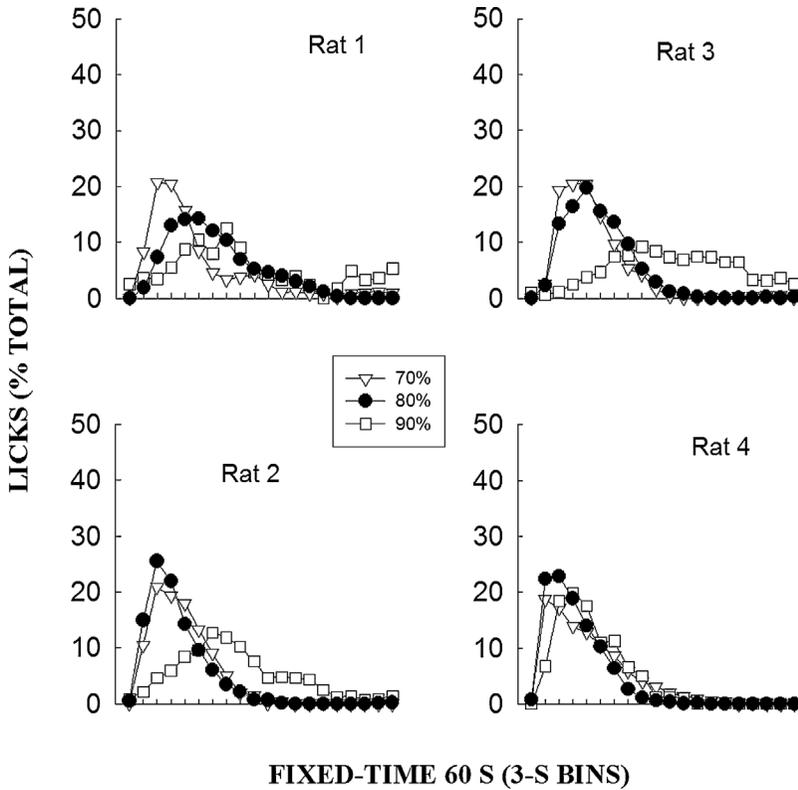


Fig. 4. Individual graphs for each rat under the FT 60-s schedule for licks at each of the different deprivation levels (70%, 80%, and 90%) across the 3-s bins of the interfood interval. The vertical axis represents the percentage of licks given per bin over the total licks in the interfood interval. The values of the points are the mean licks over the last five sessions of the respective experimental stages.

although our findings suggest that on reaching a given weight reduction level sufficient to generate a strong drinking response (80% in our study), conditions of greater severity do not further increase adjunctive drinking.

Schedule-induced drinking is known to be a function of the duration of the interfood interval. If this interval is too short or too long, adjunctive drinking decreases (Falk, 1966; Flory, 1971). Thus, Flores and Pellón (1995), on subjecting rats at 80% of their free-feeding weight to the FT 15-, 30-, 60-, 120-, 240- and 480-s schedules, and measuring adjunctive drinking in licks per min, found that the schedule which generated the most polydipsic drinking was the FT 30-s schedule, with the FT 15- and 60-s schedules generating intermediate rates, and the FT 120-, 240- and 480-s schedules the lowest rates. However, the graphs shown in Figure 1 do not altogether reflect this function: The trend at the 80% reduction level indicates that the most

polydipsic schedule was the FT 15-s schedule, followed by the FT 30-s schedule, and that the least polydipsic was the FT 60-s schedule, with this trend also being in evidence at the 70% reduction level, except for Rat 4 whose most polydipsic schedule was the FT 60-s schedule. It might be postulated that these differences could be due to the present rats having had experience with FT 30-, 45- and 60-s schedules (but not FT 15 s). This possibility appears unlikely, however, because the FT 15-s schedule induced more, not less drinking, thus suggesting that the rats adapted quite quickly to the new schedule. Flores and Pellón's experiment (1995) was between-subjects, and the present experiment was within-subjects with repeated exposures to the FT 15-, 30- and 60-s schedules at different levels of deprivation. This difference provides a more plausible explanation for the differences in results because in the present study all rats experienced all interfood intervals and this

could have facilitated drinking as the schedule got richer (Jacquet, 1972). In any event, and as pointed out above, the linear relationships that relate adjunctive drinking rates to interfood interval duration are in line with predictions of a positive reinforcement theory based on the notion of delay gradients (Killeen & Pellón, 2013). Furthermore, according to this theory there should be no differences in nature between the lower rate of drinking observed at long interfood intervals and the higher rate of drinking induced at short intervals (as suggested, for example, by Flores & Pellón, 1997). According to this theory, differences in drinking rates should be due to the time from the behavior to the upcoming food, reflecting the delay-of-food gradient.

Turning to the molecular data (see Figs. 2, 3 and 4), it can be seen that, at the 80% and 70% reduction levels, the distribution of adjunctive drinking generally underwent little change in response to a lengthening of the interfood interval, and that the position of the peak was only affected to a limited degree for the 80% level. Overall, the distributions were those that would be expected for schedule-induced drinking, and were similar to, for instance, those observed by Flores and Pellón (1997) in an experiment in which they exposed rats, at an 80% reduction level, to FT 15-, 30- and 60-s schedules, among others.

It can be seen, both from the results of the present experiment at the 80% deprivation level and from the data reported by Flores and Pellón (1997), that there is a trend toward the peak shifting to the right in response to an increase in interfood interval duration. Other authors have reported similar results (Rosellini & Burdette, 1980; Segal, Oden, & Deadwyler, 1965; Shurtleff, Delamater, & Riley, 1983). Even so, it should not be overlooked that the results of the present experiment indicate that the shift at the 80% reduction level was limited and smaller than that at the 90% level, and that the shift was practically nonexistent at the 70% level.

Accordingly, our results would seem to indicate that in schedule-induced drinking the trend for the peak to shift to the right in response to a lengthening of the interval is much more pronounced when the motivational level is low than when it is high. In this respect, the results of the present experiment are consistent with the results and conclusions reached by Campagnoni, Lawler, and Cohen

(1986) making it possible to conclude that schedule-induced drinking at low motivational levels would resemble behavior akin to general activity, whereas schedule-induced drinking at high motivational levels (70% and 80%) is more like schedule-induced attack in pigeons at 75% of their free-feeding weight (i.e., with a comparatively far smaller shift). The distribution of general activity was flatter than that of induced attack, and the peak tended to be situated farther to the right; likewise in the present experiment lick distribution was flatter for low than for high motivational levels and the response peak tended to be situated farther to the right. Differences in both cases were more marked as the interfood interval grew longer.

On making a comparison between the molar and molecular data, and excluding Rat 4, it can be seen that when it comes to comparing the different deprivation levels, when the molar data are considered, the shorter the interfood interval, the greater the differences; and if the molecular data are considered, the longer the interfood interval, the greater the difference in the position of the response peak. Thus, in terms of sensitivity to the level of deprivation, these two different ways of approaching the analysis of adjunctive drinking appear to interact in opposite ways in response to an increase in the duration of the interfood interval.

The licking rate and the distribution of licking do appear to be modulated differently by food deprivation. For example, while Rat 1 registered very different licking rates under the FT 15-s schedule at 80% versus 90% food deprivation (see Fig. 1, upper-left panel), the temporal distributions were nonetheless very similar (see Fig. 2, upper-left panel). Similarly, changes in temporal distributions without changes in overall responding rates occurred in other rats; for example, although Rat 3 under the FT 30-s schedule displayed marked changes in licking distributions with changes in food deprivation (see Fig. 3, upper-right panel), no such marked differences were found in the overall licking rates (see Fig. 1, upper-right panel).

The current study shows that food deprivation has effects on schedule-induced drinking that depend on the duration of the interfood interval, and this might lead to a different interpretation of the results of a previous study from our laboratory which showed a modulation of schedule-induced drinking by

food deprivation when licks initiated delays in food delivery (Lamas & Pellón, 1995). The present study showed that the higher the food deprivation, the less effective were the delays in reducing drinking, thus resulting in greater increases in interfood interval duration as food deprivation increased. The general tendency of higher food deprivation to result in higher schedule-induced drinking does not seem to apply to interfood intervals exceeding certain lengths, as the present results showed with the longest FT schedules. This supports the interpretation offered by Lamas and Pellón that in their case food deprivation acted specifically on behavior maintained by food delays and not by more general effects on level of responding.

References

- Allen, J. D., & Kenshalo, D. R. (1976). Schedule-induced drinking as a function of interreinforcement interval in the rhesus monkey. *Journal of the Experimental Analysis of Behavior*, *26*, 257–267.
- Azrin, N. H., Hutchinson, R. R., & Hake, D. F. (1966). Extinction-induced aggression. *Journal of the Experimental Analysis of Behavior*, *9*, 191–204.
- Bolles, R. C. (1961). The interaction of hunger and thirst in the rat. *Journal of Comparative and Physiological Psychology*, *54*, 580–584.
- Campagnoni, F. R., Lawler, C. P., & Cohen, P. S. (1986). Temporal patterns of reinforcer-induced general activity and attack in pigeons. *Physiology and Behavior*, *37*, 577–582.
- Falk, J. L. (1961). Production of polydipsia in normal rats by an intermittent food schedule. *Science*, *133*, 195–196.
- Falk, J. L. (1966). Schedule-induced polydipsia as a function of fixed interval length. *Journal of the Experimental Analysis of Behavior*, *9*, 37–39.
- Falk, J. L. (1967). Control of schedule-induced polydipsia: Type, size and spacing of meals. *Journal of the Experimental Analysis of Behavior*, *10*, 199–206.
- Falk, J. L. (1969). Conditions producing psychogenic polydipsia in animals. *Annals of the New York Academy of Sciences*, *157*, 569–593.
- Flores, P., & Pellón, R. (1995). Rate-dependency hypothesis and the rate-decreasing effects of *d*-amphetamine on schedule-induced drinking. *Behavioural Pharmacology*, *6*, 16–23.
- Flores, P., & Pellón, R. (1997). Effects of *d*-amphetamine on temporal distributions of schedule-induced polydipsia. *Pharmacology, Biochemistry and Behavior*, *57*, 81–87.
- Flory, R. K. (1971). The control of schedule-induced polydipsia: Frequency and magnitude of reinforcement. *Learning and Motivation*, *2*, 215–227.
- Freed, E. X., & Hymowitz, N. (1972). Effects of schedule, percent body weight and magnitude of reinforcer on schedule-induced polydipsia. *Psychological Reports*, *31*, 95–101.
- Jacquet, Y. F. (1972). Schedule-induced licking during multiple schedules. *Journal of the Experimental Analysis of Behavior*, *17*, 413–423.
- Keehn, J. D., & Stoyanov, E. (1986). The development of adjunctive drinking by rats: Conditioned and unconditioned components. *Animal Learning and Behavior*, *14*, 411–415.
- Killeen, P. R., & Pellón, R. (2013). Adjunctive behaviors are operants. *Learning and Behavior*, *41*, 1–24.
- Lamas, E., & Pellón, R. (1995). Food-deprivation effects on punished schedule-induced drinking in rats. *Journal of the Experimental Analysis of Behavior*, *64*, 47–60.
- Palya, W. L. (1993). Bipolar control in fixed interfood intervals. *Journal of the Experimental Analysis of Behavior*, *60*, 345–359.
- Pellón, R. (1990). Polidipsia inducida por programa: I. Definición y marco conceptual [Schedule-induced polydipsia: I. Definition and conceptual framework]. *Revista de Psicología General y Aplicada*, *43*, 313–326.
- Pellón, R. (1992). Polidipsia inducida por programa: II Variables motivacionales [Schedule-induced polydipsia: II. Motivational variables]. *Revista de Psicología General y Aplicada*, *45*, 251–266.
- Pellón, R., & Pérez-Padilla, A. (2013). Response-food delay gradients for lever pressing and schedule-induced licking in rats. *Learning and Behavior*, *41*, 218–227.
- Reid, A. K., & Staddon, J. E. R. (1990). Mechanisms of schedule entrainment. In S. J. Cooper & C. T. Dourish (Eds.), *Neurobiology of stereotyped behavior* (pp. 200–231). New York: Oxford University Press.
- Rosellini, R. A., & Burdette, D. R. (1980). Meal size and intermeal interval both regulate schedule-induced water intake in rats. *Animal Learning and Behavior*, *8*, 647–652.
- Schaeffer, R. W., & Salzberg, C. (1973). Licking response distributions associated with the acquisition of schedule-induced polydipsia. *The Bulletin of the Psychonomic Society*, *2*, 205–207.
- Segal, E. F., Oden, D. L., & Deadwyler, S. A. (1965). Determinants of polydipsia: IV. Free reinforcement schedules. *Psychonomic Science*, *3*, 11–12.
- Shurtleff, D., Delamater, A. R., & Riley, A. L. (1983). A reevaluation of the CS-hypothesis for schedule-induced polydipsia under intermittent schedules of pellet delivery. *Animal Learning and Behavior*, *11*, 247–254.
- Staddon, J. E. R. (1977). Schedule-induced behavior. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 125–152). Englewood Cliffs, NJ: Prentice-Hall.
- Staddon, J. E. R., & Ayres, S. L. (1975). Sequential and temporal properties of behavior induced by a schedule of periodic food delivery. *Behavior*, *54*, 26–49.
- Staddon, J. E. R., & Simmelhag, V. L. (1971). The “superstition” experiment: A reexamination of its implications for the principles of adaptive behavior. *Psychological Review*, *78*, 3–43.
- Stein, L. (1964). Excessive drinking in the rat: Superstition or thirst? *Journal of Comparative and Physiological Psychology*, *58*, 237–242.
- Stricker, E. M., & Adair, E. R. (1966). Body fluid balance, taste and post-prandial factors in schedule-induced polydipsia. *Journal of Comparative and Physiological Psychology*, *62*, 449–454.

Received: January 7, 2013

Final Acceptance: August 15, 2013

Appendix 1

Mean for the last five sessions of licks by each rat in 3-s bins under the FT 15-s schedule as shown in Figure 2.

Bins	Rats 70%				Rats 80%				Rats 90%			
	1	2	3	4	1	2	3	4	1	2	3	4
1	13.2	6.8	10.2	29.6	11.9	13.0	0.2	67.2	12.4	1.6	7.8	12.2
2	234.8	60.3	103.5	68.6	90.2	102.4	44.2	210.6	14.8	9.4	9.6	26.4
3	190.8	72.5	135.1	68.8	144.1	100.6	79.0	185.6	23.2	25.0	9.1	54.8
4	115.8	65.3	117.7	53.0	127.0	66.4	58.2	118.8	17.8	24.4	12.9	35.2
5	55.2	29.8	84.5	35.2	85.0	37.4	30.2	65.0	16.6	15.0	9.9	22.4

Appendix 2

Mean for the last five sessions of licks by each rat in 3-s bins under the FT 30-s schedule as shown in Figure 3.

Bins	Rats 70%				Rats 80%				Rats 90%			
	1	2	3	4	1	2	3	4	1	2	3	4
1	3.4	9.4	3.0	19.2	0.2	16.1	0.2	18.4	8.2	2.0	6.2	0
2	158.7	89.2	61.9	163.6	20.0	123.7	55.8	144.4	7.0	6.9	5.4	27.8
3	168.9	99.6	100.5	183.4	50.0	127.3	98.4	131.4	39.2	11.0	6.2	50.6
4	110.9	75.0	90.9	150.2	50.8	72.3	102.0	97.0	43.4	16.6	16.8	35.6
5	83.2	53.4	73.8	107.2	58.4	32.2	65.2	41.2	34.0	21.1	26.2	24.8
6	45.8	19.2	54.9	67.6	46.2	8.3	29.0	11.8	25.8	18.9	32.8	9.6
7	17.0	6.6	42.2	34.4	35.0	3.8	3.0	0.6	9.6	17.6	32.4	8.6
8	7.5	3.6	34.8	21.6	22.8	0	0	0	14.6	12.0	30.6	4.4
9	8.5	1.8	25.4	13.8	10.8	0.2	0	0	12.0	9.9	24.4	0.8
10	2.4	0	18.7	6.0	9.8	0.4	0	0	12.6	11.0	16.2	1.8

Appendix 3

Mean for the last five sessions of licks by each rat in 3-s bins under the FT 60-s schedule as shown in Figure 4.

Bins	Rats 70%				Rats 80%				Rats 90%			
	1	2	3	4	1	2	3	4	1	2	3	4
1	0	0.4	0	8.9	0	2.6	0	4.4	3.2	1.0	1.6	0
2	30.6	36.8	10.6	308.6	9.8	81.0	6.4	133.4	4.6	2.6	1.0	9.2
3	76.1	73.7	82.0	282.9	38.2	138.5	37.6	136.4	4.4	5.7	2.0	25.2
4	74.6	68.5	86.9	229.4	67.6	119.0	46.2	112.6	7.0	7.3	4.2	27.2
5	57.8	63.3	86.6	211.2	73.4	77.4	55.6	83.2	11.2	10.3	6.6	24.0
6	31.2	46.9	62.6	171.6	74.0	52.2	43.8	61.4	13.4	11.7	8.2	15.0
7	16.6	31.9	41.4	142.8	62.6	32.6	38.4	38.0	10.2	15.6	13.0	15.4
8	12.0	17.8	22.4	95.6	53.8	18.6	27.2	15.6	16.0	14.5	13.4	9.0
9	14.0	7.0	18.2	64.4	36.0	11.6	14.6	6.2	11.6	12.5	16.2	6.8
10	15.4	5.4	6.8	51.4	27.0	4.0	8.2	3.6	6.0	9.3	14.8	1.6
11	9.0	0.2	1.2	31.0	23.8	3.6	3.2	2.0	5.0	5.7	12.8	1.6
12	4.0	1.2	0	23.0	21.0	0.4	2.2	0.2	4.2	5.9	12.0	1.4
13	4.2	0	0.2	14.0	15.4	0	0.6	0.6	5.0	5.7	13.0	0
14	3.0	0	0.6	8.9	11.0	0	0	0	3.0	5.3	12.8	0.4
15	3.0	0.2	0.4	5.6	6.2	0	0	0	0	3.0	11.4	0.2
16	1.0	0	1.4	0.2	1.8	0	0	0	2.2	1.4	11.4	0
17	3.0	0	1.4	1.0	0	0	0	0	6.2	1.6	5.8	0
18	3.6	0	2.0	0.2	0	0	0.6	0	4.2	0.8	5.4	0
19	4.2	0	1.8	0	0	0.4	0	0	4.6	1.0	6.2	0
20	3.4	0	0	0.2	0	1.0	0.6	0	6.8	1.6	4.4	0