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SCHEDULE-INDUCED DRINKING: ELICITATION, ANTICIPATION, OR BEHAVIORAL INTERACTION?

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We carried out five experiments with rats on fixed-time schedules in order to define the relation between drinking and individual food-pellet presentations. In Experiment 1, unsignaled extra food occurred at the end of occasional fixed intervals, and we compared subsequent drinking patterns with drinking before the extra food presentation. In Experiment 2 we presented signaled and unsignaled extra food and measured elicited and anticipatory drinking patterns. In Experiment 3, we observed the persistence of modified drinking patterns when several consecutive intervals ended with extra pellets. In Experiments 4 and 5, we varied the magnitude of food delivery across (rather than within) sessions to replicate published findings. Results show that schedule-induced drinking is neither elicited by food presentations nor induced by stimuli associated with a high food rate. All subjects seemed to follow a simple rule: during any stimulus signaling an increase in the local probability of food delivery within a session, engage in food-related behavior to the exclusion of drinking. Schedule-induced drinking appears to be the result of dynamic interactions among food-related behavior, drinking, and other motivated behavior, rather than a direct effect of the contingencies of food reinforcement.

Key words: Schedule-induced drinking, adjunctive behavior, interim activities, response interactions, reinforcer magnitude, inhibition, rats

Intermittent presentation of food to hungry rats causes two main classes of activity to increase above their baseline (no-food) levels: the terminal response (food-related activity of some kind) and interim activities. If water is available, drinking is the most striking and reliable interim activity (Falk, 1969).

Two features of this schedule-induced polydipsia have excited research interest: its excessive quantity and the temporal regularity of drinking (and other activities) within the interfood interval when food presentation is periodic. The most notable feature of drinking and other interim activities on periodic schedules is their restriction to periods when food delivery is improbable.

Most attention has been directed to the excessive nature of schedule-induced drinking. For example, Roper (1980) writes:

> the phenomenon that is most in need of attention is the fact that a high rate of drinking is sustained over a session lasting several hours. The fact of post-reinforcement drinking *per se* is not particularly surprising, because the rat might as well drink as do anything else during the interreinforcement interval, especially since drinking is a response that is known to be closely associated with eating. (p. 168)

Roper's comment illustrates a common theme in many theories of the phenomenon: the hypothesized "special relationship" between drinking and eating. This paper tests two possible forms such a special relationship might take.

The first possibility is that drinking is to some degree elicited by eating. This is explicit in the discredited postprandial hypothesis (Lotter, Woods, & Vasselli, 1973) and plays a subordinate, but necessary, part in several other theories (cf. review in Staddon, 1977a). After all, if drinking is not "closely associated with eating," why should rats drink rather than run or (as pigeons do) attack? Experiments in which a stimulus other than food bears a similar predictive relation to food delivery have generally found less poststimulus drinking following the nonfood stimulus (Alferink, Bartness, & Harder, 1980; Allen & Por-

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ter, 1977; and Rosenblith, 1970). These studies seem to imply a food-elicited component to schedule-induced drinking. Our first three experiments attempt to demonstrate that increments in food-portion size can elicit drinking on periodic-food schedules.

The second possible relation between food and schedule-induced drinking derives from the generally positive relation between the total amount of drinking and factors related to food motivation. For example, if session length is controlled, amount of drinking is positively related to frequency of food delivery over a wide range of food rates (e.g., Hawkins, Schrot, Githens, & Everett, 1972; review in Staddon, 1977a). Amount of drinking on periodic schedules is also inversely related to body weight (Freed & Hymowitz, 1972; Roper & Nieto, 1979; Wayner & Rondeau, 1976). Many studies (Bond, 1973; Couch, 1974; Flory, 1971; Millenson, 1975; Rosellini & Burdette, 1980; Rosenblith, 1970) have shown a positive relation between food magnitude and amount of drinking, although others have found that induced drinking is independent of, or even inversely related to, food magnitude (Freed & Hymowitz, 1972; Keehn & Colotla, 1970, 1971; Yoburn & Flory, 1977). Although the magnitude studies are a little inconsistent, these results suggest that the anticipation of food—that is, stimuli associated with high rates of food delivery—may have a facilitating effect on drinking (cf. Kissileff, 1969). The later experiments in this study address this possibility.

Our experiments provide no evidence for either an eliciting or an anticipatory effect of food delivery on schedule-induced drinking. We are forced to conclude that interactions at some other level among food-related behavior, "other" activities, and drinking may be responsible both for the occurrence of drinking (as opposed to other possible interim activities) and for its excessive level.

EXPERIMENT 1
EFFECTS OF UNPREDICTABLE INCREASES IN MEAL SIZE

If food delivery has even a modest eliciting effect, then occasional, unpredictable increases in meal size on a fixed-time schedule might be expected to provoke some increase in schedule-induced drinking, either in the interfood interval following the increase, or perhaps in some later interval. We tested this idea in a pilot study in which we gave four rats extensive training on a fixed-time 30-sec schedule of food presentation and later increased the number of pellets delivered within two of the 30-sec intervals. Each subject received a minimum of 10 extra-food sessions and a minimum of 10 sessions in which no extra food was delivered. A microprocessor stored the time of occurrence of every lick, head-in, and head-out of the feeder opening, so that interval-by-interval averages over sessions within a condition could be obtained. A comparison of post-extra-food drinking versus (a) pre-extra-food drinking and (b) drinking in the corresponding interfood interval in control sessions indicated that extra food delivery always resulted in reduced drinking for two or three succeeding interfood intervals. This result is surprising, since most experiments have shown that increases in the magnitude of food facilitate schedule-induced drinking.

The pilot study yielded the surprising result that rats drank substantially less after intervals ending with six pellets than after intervals ending in one pellet. The present study replicates this finding and incorporates several control conditions. We asked: (a) does extra food increase or decrease subsequent drinking? (b) what is the effect of water availability during the extra food presentations? and (c) what is the effect of different temporal spacings between the extra food pellets?

METHOD

Subjects

Four female rats (three albino rats, approximately 120 days old, reared in this laboratory, and one Charles River hooded rat approximately 150 days old at the beginning of the pilot study) were housed individually in one room with 24-hr light. Each subject had been trained on a fixed-time 30-sec (FT 30) schedule for at least 28 sessions. Their ad lib. weights were determined before training by averaging each subject's weight over three consecutive days. Their weights were reduced to 80% of their free-feeding weights over a period of six days. Water was freely available in the home cages.

Apparatus

The octagonal apparatus depicted in Figure 1 was used. All areas other than the feeding area, the center, and the area containing a retractable drinking tube were blocked off. The distance between the feeder opening and the tip of the drinking tube was 66 cm. The tip of the metal drinking tube was recessed .3 cm behind the clear Plexiglas wall, and all except the tip was electrically insulated. The contact-lickometer circuitry was designed by Alliston K. Reid and required less than .7 microamperes for operation. The apparatus was located in a large homemade sound-attenuating chamber, and white noise was present during all sessions. Noyes 45-mg pellets, Formula M, were dispensed throughout all experiments.

A photocell in the food hopper monitored head in and head out of the hopper. A microprocessor recorded every discrete event (licking, head in hopper, and head out of hopper) and their times of occurrence with $\frac{1}{60}$-second resolution. These data were later transferred to diskettes for analysis by a PDP-11 minicomputer. Subjects were usually monitored informally via closed-circuit television.

Procedure

All subjects were run seven days a week in all experiments. The 28 training sessions consisted of a FT-30 sec schedule of food presentation with access to a drinking tube. Each session began with a pellet delivery and ended with the 100th pellet delivery (99 interpellet intervals for a session length of 49.5 min). The pattern of polydipsic drinking that developed was considered stable for each subject when the percentage of intervals containing drinking failed to drop below 75% on any day for 10 consecutive days, and the number of licks per session was relatively constant.

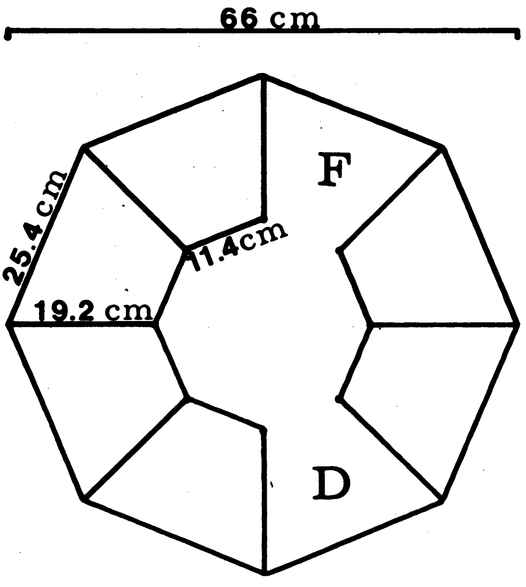

Fig. 1. The octagonal apparatus was used with all areas other than the Feeder Area, "F," and the Drinking Area, "D," blocked off, as depicted. The drinking tube and pellet dispenser were located on the outside walls. The inside walls which blocked off unused compartments were made of white Plexiglas.

All subjects were shifted to the pilot-study procedure for about 10 days. In each session, 2 of the 99 fixed-time intervals ended in six pellets (Intervals 30 and 70), the rest ended in one pellet. This procedure is described later as Condition EF-S ("*e*xtra *f*ood, *s*paced") in Figure 2.

Immediately following the pilot study, all four subjects were shifted to the experimental procedure. Six different conditions were presented, one per day, in a random order without replacement (randomized blocks of six), until all subjects had received eight sessions of each condition. The differences between conditions were solely in Intervals 30 and 70 (with concomitant variation in session length, since sessions ended after 100 pellets—all sessions were either 49.5 or 45.5 min long). The conditions, shown in Figure 2, were as follows:

(1) Baseline (B): FT-30 sec with no modification to any intervals.
(2) Extra Food, Spaced (EF-S): in Intervals 30 and 70, five extra pellets spaced 5 sec apart were delivered.
(3) No Water (W): in Intervals 30 and 70, the drinking tube was retracted for the entire interpellet interval. There was no modification of pellet delivery.
(4) Extra Food, Spaced, No Water (EF-S-W): a combination of Conditions EF-S and W in which five extra pellets were delivered and the drinking tube was retracted.

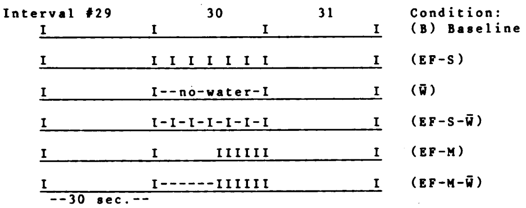

Fig. 2. Event diagram depicting the conditions presented in Experiment 1. The conditions are described in the text.

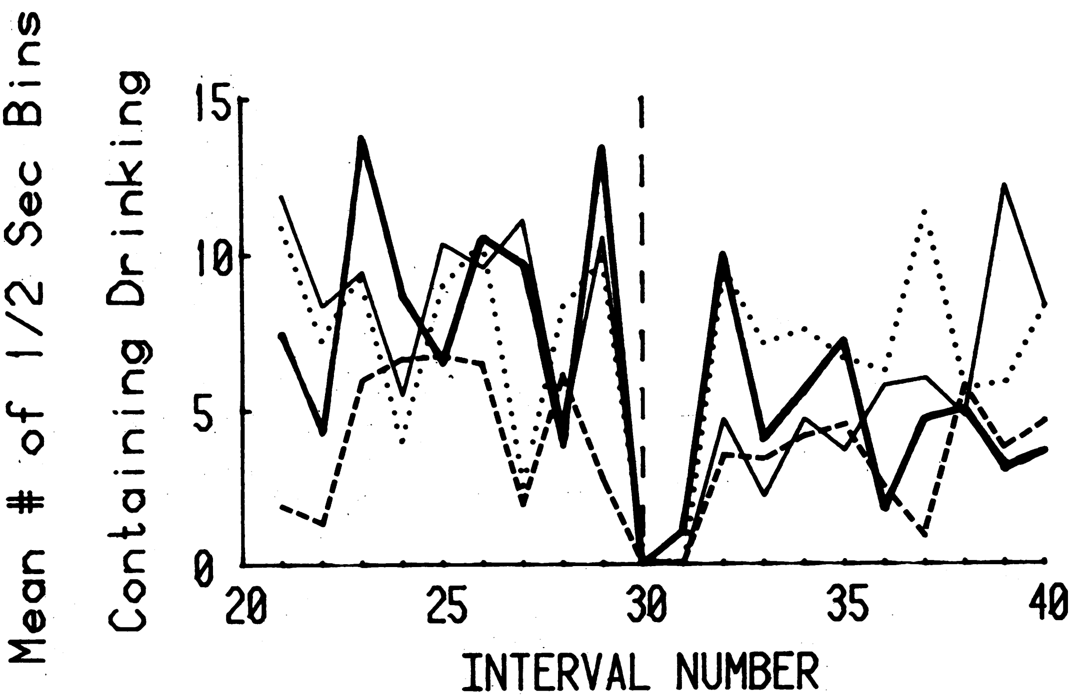

Fig. 3. Mean number of ½-second bins containing licking in each FT 30-sec interval before, during, and after presentations of five extra pellets in Interval 30 (Condition EF-S). Curves represent the amount of drinking for individual subjects averaged over the last eight days of exposure to Condition EF-S. Maximum on ordinate for FT 30-sec intervals = 60.

(5) Extra Food, Massed (EF-M): five extra pellets were delivered spaced 1 sec apart beginning 25 sec into the interval.

(6) Extra Food, Massed, No Water (EF-M-W): in Intervals 30 and 70, a combination of Conditions W and EF-M, five extra pellets were delivered spaced 1 sec apart beginning 25 sec into the interval, and the drinking tube was withdrawn for the interval duration.

Supplemental food (Purina Rat Chow) was given to each subject several hours after each session to maintain body weight at 80%.

RESULTS

Every presentation of extra food resulted in substantial reductions in drinking. Figure 3 shows this result. The abscissa refers to the interval number within the session, and the vertical dashed line represents the interval in which a manipulation was made (Interval 30). The ordinate represents the mean number of ½-sec bins within each interpellet interval that contained licking (maximum per interval on FT 30-sec = 60). The figure shows that all subjects reduced their drinking levels in Condition EF-S in similar fashion (each curve represents eight days for each subject). For brevity we show only the first test interval; the results of the manipulations in the second test interval (Interval 70) were exactly the same.

The curves in Figure 3 are in terms of proportion of ½-sec bins containing a lick; the pattern of results is the same in terms of local lick rate, however. We use the temporal scale so that drinking can easily be compared to head-in-feeder, which cannot be measured as a rate.

The top panel in Figure 4 shows the amounts of drinking per interval for the eight days of each condition averaged for all subjects in Conditions B, EF-S, W, and EF-S-W. A comparison of Condition EF-S (heavy dashed line), in which five extra pellets were spaced 5 sec apart, with baseline (heavy solid line) in Intervals 31 and 71 indicates a dramatic reduction in drinking. This reduction is not evident in Condition W (light solid line), in which the drinking tube was withdrawn for the interval duration, so it cannot be attributed to the reduction in drinking in Intervals 30 and 70 when the extra food was delivered.

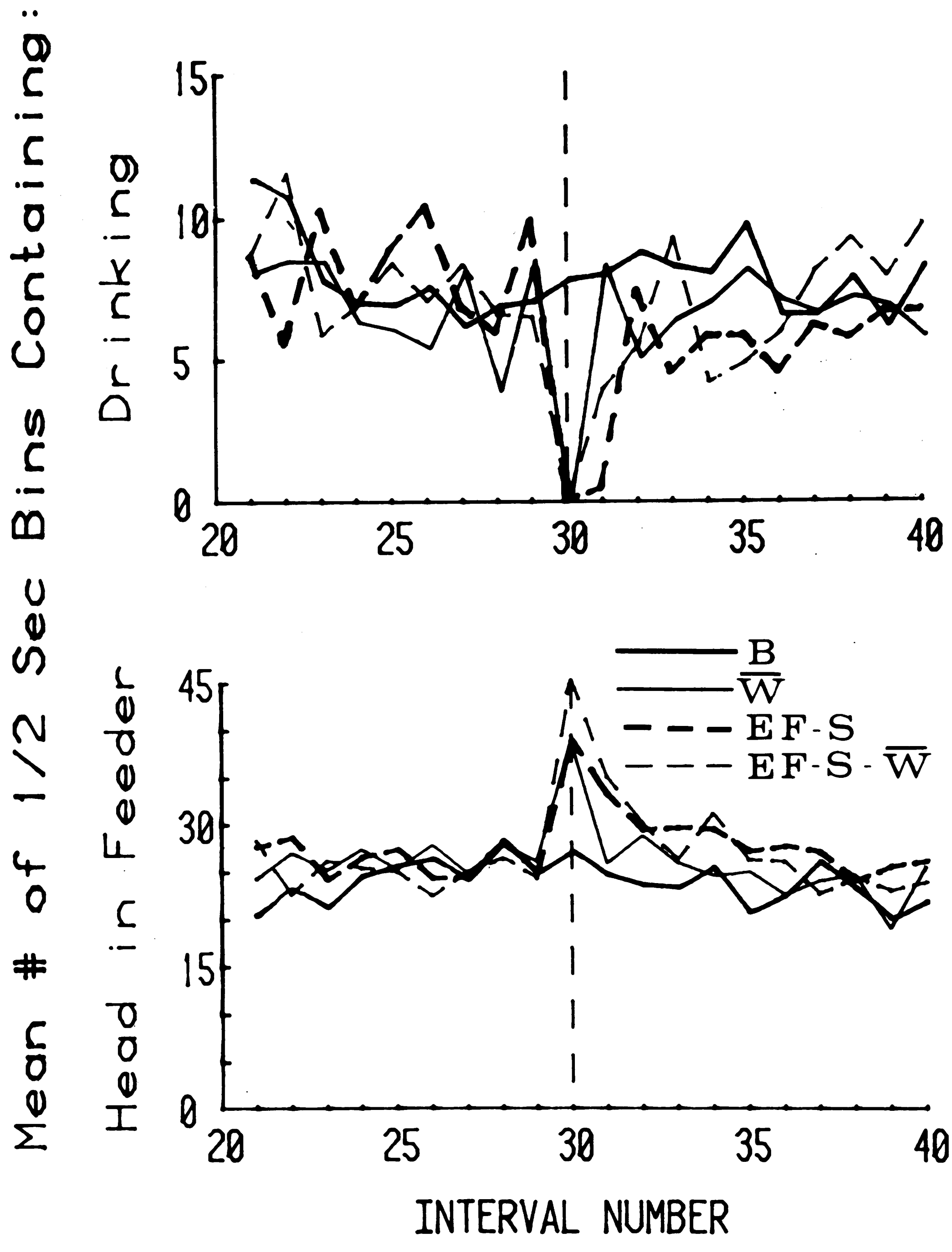

Fig. 4. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for consecutive FT 30-sec intervals for Conditions B, EF-S, W, and EF-S-W. The vertical dashed line at Interval 30 represents the interval in which the appropriate manipulation was made.

The bottom panel in Figure 4 shows the time spent with the subjects' heads in the feeder opening, blocking the photo-beam. These curves are approximately the complements of the corresponding curves in the upper graph. Clearly, most of the time subtracted from drinking was added to the time spent engaged in food-related activities.

Figure 5 shows the changes in drinking and feeder activity in Conditions B, W, EF-M, and

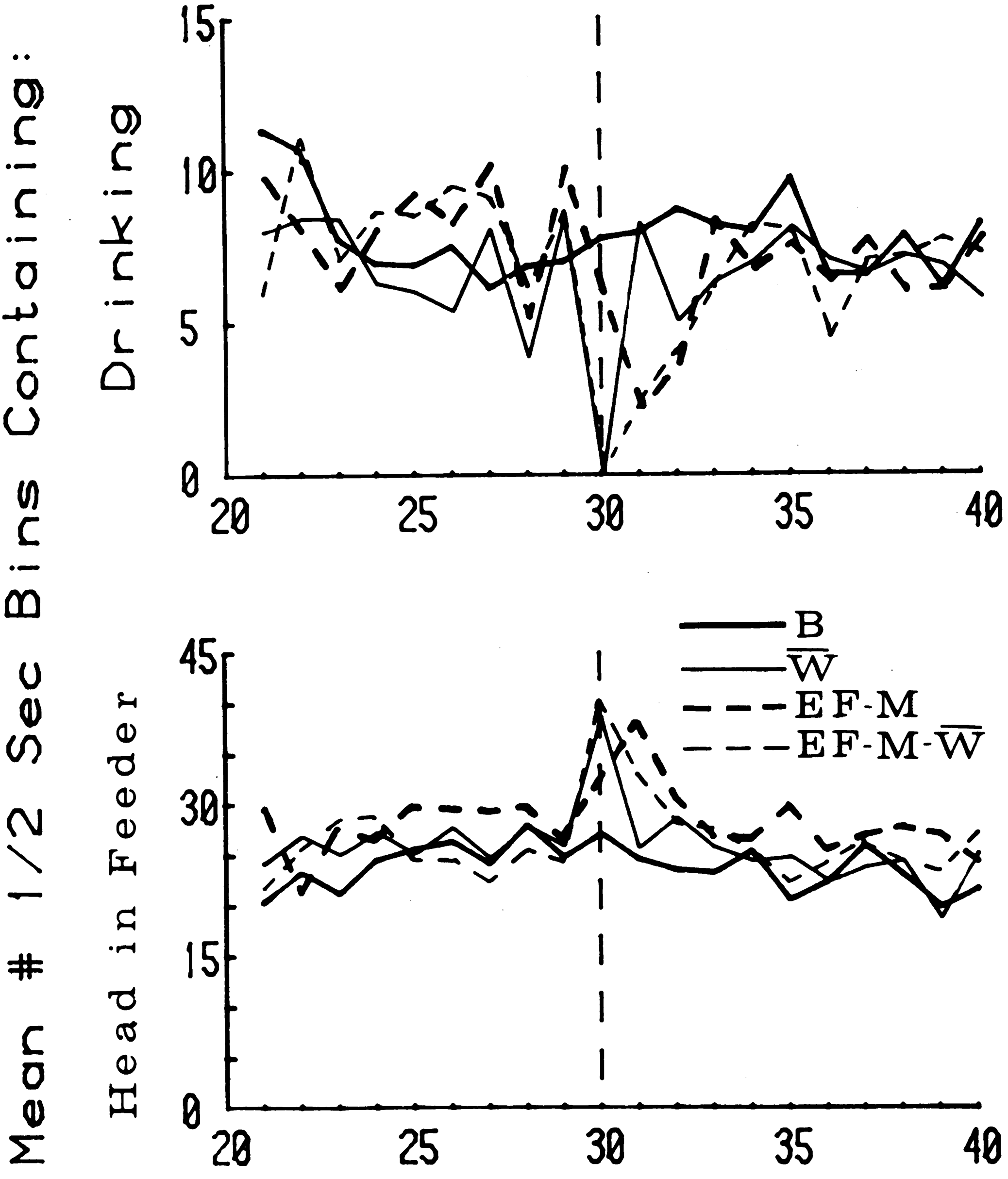

Fig. 5. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for consecutive FT 30-sec intervals for Conditions B, EF-M, W, and EF-M-W.

EF-M-W. The manipulations made in these conditions differ from those just discussed only in the temporal spacing of the extra food. The results from Conditions EF-M and EF-M-W replicated the previous findings: the extra food resulted in reduced drinking but increased feeder activity. As in the other conditions, drinking following extra food plus tube withdrawal was slightly greater than following extra food alone.

Comparison of the drinking levels (see Figure 6) between Condition EF-S, in which the five extra pellets were spaced 5 sec apart (Spaced), and Condition EF-M, in which they

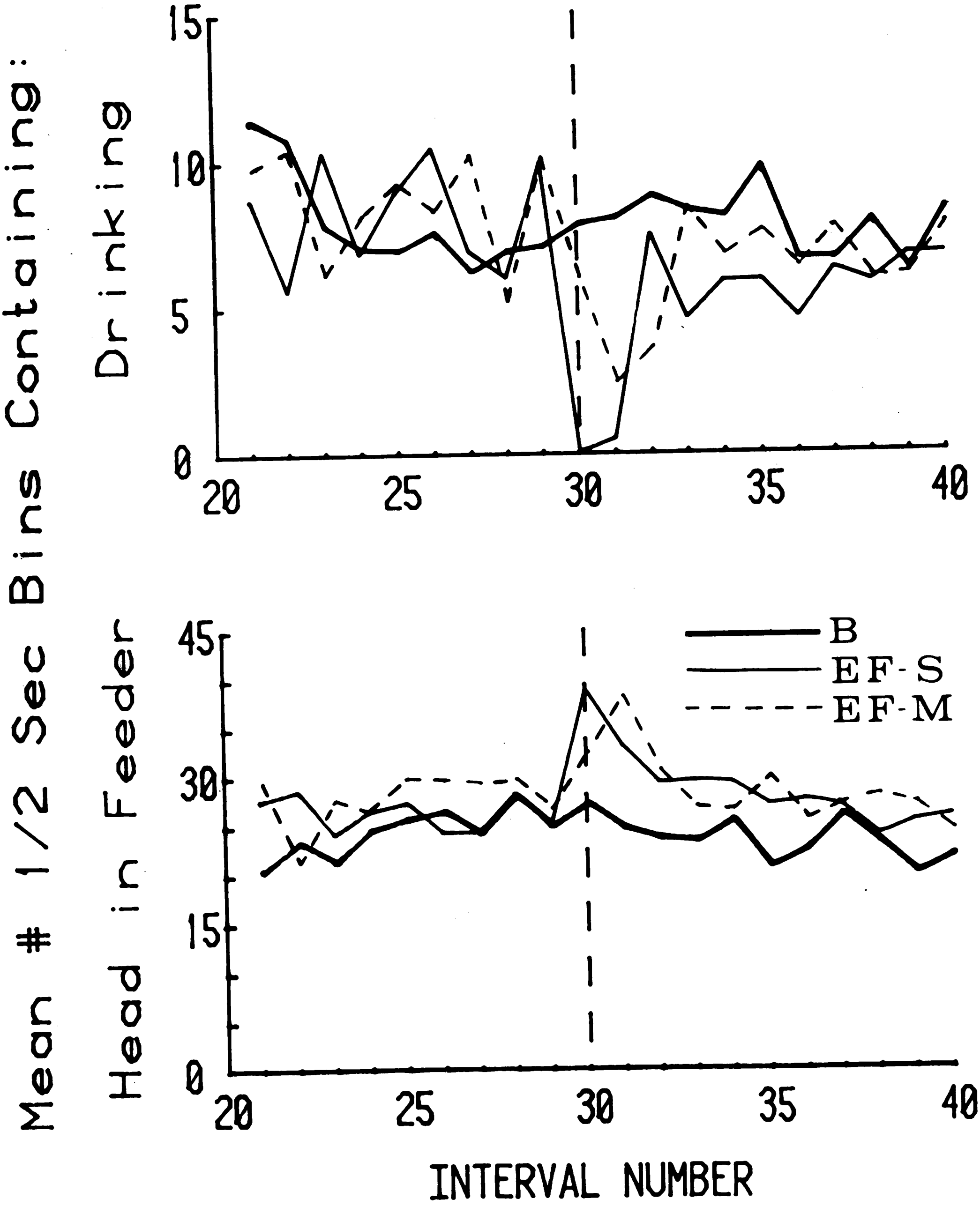

Fig. 6. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for consecutive FT 30-sec intervals for Conditions B, EF-S, and EF-M.

were spaced 1 sec apart (*M*assed) demonstrates less drinking with 5-sec spacing. This difference in drinking levels is due to different recovery rates: the rats resumed drinking in Interval 31 earlier following massed than following spaced extra food in Interval 30.

The individual and mean numerical data for drinking and head-in-feeder in Interval 31 for all six conditions are shown in Tables 1 and 2. The modal rank ordering in terms of amount of drinking in Interval 31 (lowest first) is EF-S < EF-M < EF-M-W < EF-S-W < W

Table 1

Mean Number of ½-Sec Bins Containing Drinking in Interval 31

	Baseline	*EF-S*	*W*	*EF-S-W*	*EF-M*	*EF-M-W*
Rat B	15.00	0.00	9.22	4.33	4.22	2.44
Rat E	7.00	1.11	8.75	2.11	1.22	1.75
Rat G	5.56	0.00	8.22	4.37	1.89	3.33
Rat H	4.57	1.00	4.00	2.56	0.00	1.00
Mean	8.04	0.53	7.55	3.34	1.83	2.13

< B; that is, least following unsignaled, spaced, extra food, then massed extra food, massed with no water, spaced with no water, no water, and finally, baseline. The individual rats deviated little from this pattern.

There was rather less agreement among animals on the amount of head-in-feeder in these six interval types, although most such behavior usually occurred in the extra-food intervals, least in the baseline and no-water intervals.

DISCUSSION

The amount of drinking following larger-than-normal magnitudes of food presentation on a FT 30-sec schedule was dramatically reduced relative to pre-extra-food levels and relative to the same temporal period in sessions with no extra food presentations. These results are incompatible with explanations of schedule-induced polydipsia as food-elicited. Our results show that although a periodic schedule of food presentation may induce excessive drinking, individual "large-meal" presentations within a session inhibit, rather than facilitate, subsequent drinking.

The rank ordering of drinking levels in Interval 31 shown in Table 1 is readily explained by the hypothesis that the level of drinking was determined entirely by the level of competing food-related activities, of which head-in-feeder was the one actually measured. Thus, drinking was least in the EF-S condition because the transition from extra food pellets at 5-sec intervals back to FT 30-sec is less abrupt than the transition from pellets at 1-sec intervals. Consequently, food-related activity induced by the extra food took longer to extinguish (hence interfered more with drinking) in the EF-S conditions than in the EF-M conditions. Similarly, the return of the water bottle in the W conditions provided a signal for the end of extra food. In consequence, less food-related behavior occurred in the EF-W conditions than in comparable conditions where no extraneous change occurred at the end of the extra-food interval.

The rank ordering of conditions in terms of amount of head-in-feeder behavior is less consistent than the ordering in terms of drinking, but this need not surprise. Head-in-feeder is only one of several possible food-related activities that the rats engaged in. For example, we saw all the rats digging or gnawing the wire floor next to the food hopper, and these actions had no effect on the feeder photocell. Since different food-related activities are probably ready substitutes for one another, it is likely that variation in one of them (head-in-feeder, for example) will be much greater than variation in the set as a whole (cf. Kagel, Battalio, Green, and Rachlin, 1980). Since the animals did little but drink and engage in food-related activities in this situation, paradoxically, drink-

Table 2

Mean Number of ½-Sec Bins Containing Head-in-Feeder in Interval 31

	Baseline	*EF-S*	*W*	*EF-S-W*	*EF-M*	*EF-M-W*
Rat B	9.67	12.44	15.11	18.11	16.22	16.78
Rat E	30.22	39.33	32.25	45.56	47.33	43.13
Rat G	17.44	23.11	10.89	20.38	43.22	16.56
Rat H	39.67	43.88	36.44	43.89	26.67	45.11
Mean	24.25	29.69	23.67	31.99	33.36	30.40

ing might well be a better (inverse) measure of the level of food-related activities than any one of those activities by itself.

If elicitation is ruled out as an explanation for schedule-induced drinking, there remains the possibility that drinking is due to anticipation of upcoming food presentation: perhaps drinking, like food-related behavior, is facilitated in some way by a stimulus that signals extra food—even though the two classes of behavior occur at different times in the presence of that stimulus. Experiment 2 examines the roles of anticipatory versus postfood drinking by looking at the amount of drinking in signaled interfood intervals that end with either one or six food pellets.

EXPERIMENT 2

THE CONTRIBUTIONS OF ELICITED AND ANTICIPATORY EFFECTS TO SCHEDULE-INDUCED DRINKING

Experiment 2 tests the hypothesis that induced drinking is anticipatory by signaling 50% of the extra-food intervals. Three comparisons will be of interest: (a) the amount of drinking in signaled vs. unsignaled extra-food intervals; (b) the amount of drinking following these two classes of interval; and, (c) the degree to which elicited and anticipatory drinking interact.

Method

Subjects

The subjects were the same as in Experiment 1.

Apparatus

A Sonalert (440-Hz tone source, 88 dB at the center of the apparatus) was added in a blocked-off area adjacent to the feeder area.

Procedure

Session length was held constant at 75 interpellet intervals of FT 30-sec. There were four test intervals in each session: Intervals 15, 30, 45, and 60. Two rats had the tone off during all except the test intervals, and the other two had the tone on during all except the test intervals.

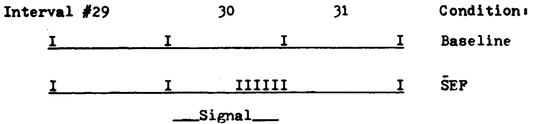

Fig. 7. Event diagram depicting the conditions presented in Experiment 2. The conditions are described in the text.

Training. Each subject was exposed to 11 or 12 consecutive sessions containing signaled intervals with extra food (Condition SEF in Figure 7) to ensure that each subject was under stimulus control.

Three different conditions were then presented in random order without replacement (randomized blocks) until each subject had been exposed to ten sessions of each condition. The conditions were:

(1) Baseline (B): normal FT 30-sec. Two rats had tone always off; the other two had tone on.
(2) Unsignaled Extra Food (SEF): FT 30-sec with unsignaled extra food (spaced 1 sec apart) in the four test intervals: tone was always off with two rats and on with the other two.
(3) Signaled Extra Food (SEF): FT 30-sec with signaled extra food (spaced 1 sec apart) in the four test intervals: the tone signaled extra food with two rats, and tone offset signaled food with the other two.

Results

Drinking in the interpellet interval with signaled extra food (Condition SEF) was drastically reduced relative to the unsignaled intervals (Condition SEF).

Figure 8 shows the group mean time spent drinking and engaged in head-in-feeder for the last eight days of each condition for all four test intervals within the session. The vertical dashed lines indicate the test intervals in which a manipulation was made. Drinking during each of the four stimulus presentations in the condition with signaled extra food (represented by the light solid line) was nearly abolished (Condition SEF). There is no indication of anticipatory drinking (i.e., increased drinking during the signaled intervals). In fact, the bottom panel of Figure 8 shows that time spent in food-related activities increased during signaled intervals, and this increase was associated with a decrease in the amount of drinking.

A striking subsidiary effect, shown by all the individuals as well as the average, is an anticipatory increase in head-in-feeder, and concomitant decrease in drinking, in the interval

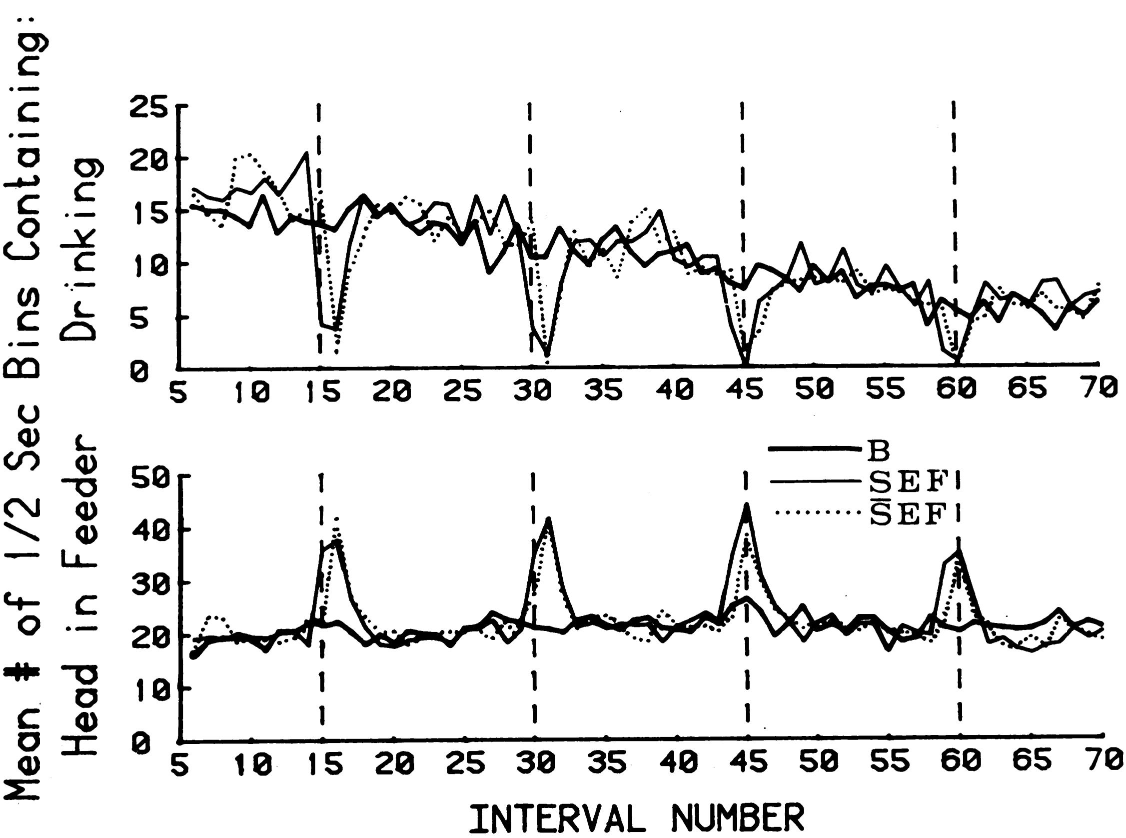

Fig. 8. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for most FT 30-sec intervals in sessions of Conditions B, SEF, and SEF. Vertical dashed lines represent the intervals in which the appropriate manipulation was made.

preceding the third and fourth test intervals in the session. When the extra-food intervals were unsignaled, this effect occurred in Intervals 45 and 60; in the signaled extra-food conditions, it occurred in Intervals 44 and 59. Figure 9 shows this effect for each individual rat.

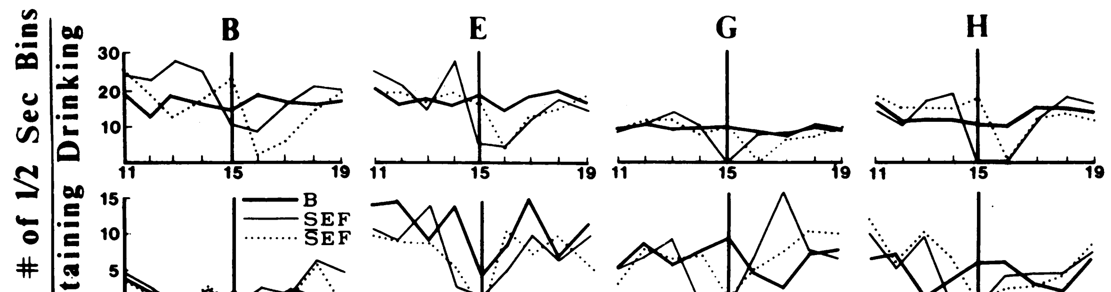

Fig. 9. Number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for most FT 30-sec intervals in sessions of Conditions B, SEF, and SEF for the four individual rats. Vertical lines represent the intervals in which the appropriate manipulation was made. Notice that the sudden decrease in drinking in conditions SEF and SEF (in Intervals 15 or 16: top panels) occurs earlier by the fourth test (in Intervals 59 or 60: bottom panels).

DISCUSSION

In all conditions in which larger-than-normal magnitudes of food were delivered, subsequent drinking was reduced relative to baseline and relative to preceding drinking levels. This decrease replicates that found in Experiment 1. At no point did drinking increase above baseline to compensate for the reductions due to extra food or signaled extra food.

The anticipatory effects in advance of the third and fourth test intervals within each session imply that the rats must have been timing or counting the intervals. The rats behaved differently on baseline and signaled and unsignaled test sessions. Since the daily sequence of conditions was determined by a randomized-block design, the rats had to reach the 15th interval before they could possibly distinguish between session (condition) types. Their failure to reduce their drinking, (a) in Interval 29 in the signaled condition, (b) in Interval 30 in the unsignaled condition, and (c) during any interval in the baseline condition, indicates that they required half of the session (or two modified intervals) to make the necessary discrimination for "setting their timer" (or counter) in that condition. We checked very carefully to see that no unintended cue was provided by the apparatus during the intervals where this anticipatory behavior occurred. It appears to represent a level of timing or counting well above that previously reported for rats and clearly deserves future study. This effect is not related to the major questions addressed by the present study, so we pursue it no further here.

In summary, all subjects decreased drinking and increased food-related behavior both in advance of, and following, signaled large-magnitude food deliveries (as in Experiment 1). Thus, this experiment provides no support for an anticipatory component in schedule-induced drinking. Taken together, Experiments 1 and 2 show that increments in meal size produce increases in food-related activities that tend to compete with, and suppress, drinking.

The results of Experiment 2 are paradoxical in showing that individual presentations of larger-than-normal magnitudes of food result in reduced drinking, even though many experiments show that large magnitudes of food presented throughout a session (i.e., at the end of every interval) result in more drinking than do smaller magnitudes. One possible explanation is that the reduction in subsequent drinking found in Experiments 1 and 2 is a function of increased competition from food-related behavior (which increases with more food), which simply masks any increase in drinking tendency. Perhaps more drinking would occur if large food magnitudes were presented for many consecutive intervals—when food-related behavior should decline, either because of habituation or reduction in hunger. Experiment 3 tests this possibility by presenting 30 intervals of signaled six pellets/interval preceded and followed by 20 intervals of one pellet/interval. This procedure allows the determination of the time-course of the reduction in drinking and eliminates any "surprising" aspect of the extra-food deliveries in Experiments 1 and 2.

EXPERIMENT 3
EFFECT OF REPEATED EXTRA-FOOD INTERVALS

The observed reduction in drinking in Experiments 1 and 2 after larger-than-normal food deliveries was of short duration. If large quantities of food were given over several consecutive intervals, drinking might at first be reduced (due to competition by food-related behavior), then, as food-related behavior wanes, might overshoot baseline, rising to above-normal levels. Such a result would indicate that the suppressive effects of extra food on drinking in the first two experiments are an artifact of the occasional and surprising pattern of the extra-food deliveries. We tested this possibility by presenting several consecutive intervals of six pellets per interval on a baseline of FT 30-sec with one pellet per interval. The hypothesis was not supported since all subjects dramatically reduced their drinking throughout the block of extra-food intervals.

METHOD

Subjects

The subjects were the same as in preceding experiments.

Apparatus

No modifications were made from Experiment 2.

Procedure

All subjects were exposed to three conditions in a random order without replacement (randomized blocks) until each subject had been exposed to at least eight sessions of each condition. Each condition was FT 30-sec with 70 interpellet intervals. The three conditions (see Figure 10) were:

(1) Baseline: Normal FT 30-sec: with two rats, the tone was always off; with the other two, the tone was always on.
(2) 20-30(W)-20: a period of twenty intervals with the drinking tube present was followed by thirty intervals with the tube retracted, then followed by twenty more intervals with the tube present. The tone was constantly on with two rats but off with the other two.
(3) 20(1)-30(6)-20(1): twenty intervals, each ending in one pellet delivery, followed by thirty intervals, each ending in six pellet deliveries, followed by twenty more intervals, each ending in one pellet delivery. For two rats, a tone accompanied the intervals ending in six pellets. For the other two rats, a tone accompanied the intervals ending in one pellet delivery.

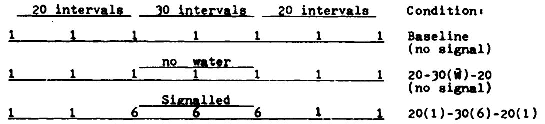

Fig. 10. Event diagram depicting the conditions in Experiment 3. The conditions are described in the text.

Results

Figure 11 shows the group mean amounts of drinking and food-related activity per interval for the last eight days of each condition over most of the session. Drinking in the baseline condition, represented by line "b," decreased across a session, whereas food-related behavior during baseline increased across each session.

Drinking was almost completely abolished during all intervals ending with six pellets [line "a" representing Condition 20(1)-30(6)-20(1)]. Drinking levels were high early in the

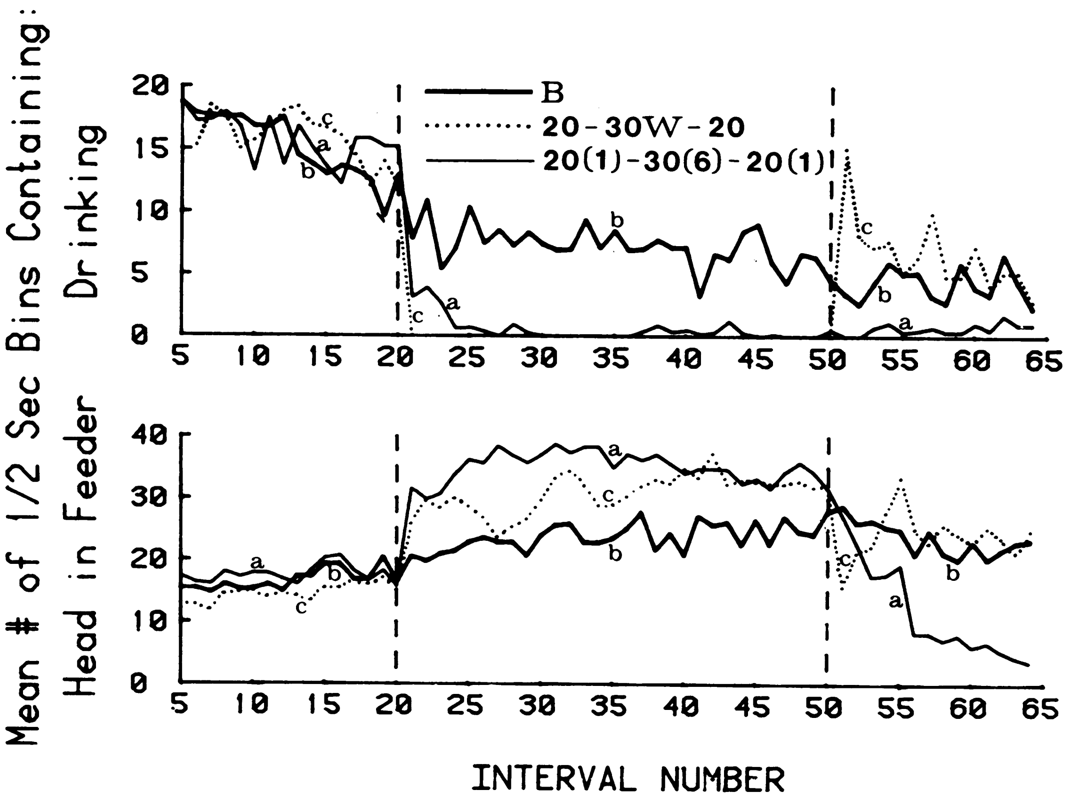

Fig. 11. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) for most FT 30-sec intervals in sessions of Conditions B, 20-30W-20, and 20(1)-30(6)-20(1). Vertical dashed lines represent transitions between blocks of interval types.

session when intervals ended with one pellet, were nearly eliminated during the six-pellet intervals, and failed to recover with the reinstatement of one pellet per interval. The failure to recover early drinking levels is possibly a function of the subjects' consumption of 201 pellets at that point. It cannot be attributed to persistence of competing food-related activities, since head-in-feeder also failed to recover.

The transition from one pellet per interval to signaled six pellets per interval resulted in an abrupt increase in food-related activity and a decrease in drinking (line "a"), demonstrating stimulus control.

The transition from six pellets per interval back to one pellet per interval resulted in a slow decrease in food-related behavior (line "a") to below any previous level.

Drinking after the reinstatement of the drinking tube in Condition 20-30(W)-20 (line "c") rebounded immediately to early levels and decreased at the same rate as during the first 20 intervals. Except for a modest overshoot in the first interval, drinking appeared to be unaffected by the prior period when water was unavailable.

DISCUSSION

Clearly, the reduction in drinking after a change to larger meals is not a transient phenomenon. Each subject reduced its drinking levels for the entire duration of the block of extra-food intervals. Drinking did not decrease for a short period and then increase above baseline levels to compensate for the reduction. The immediate reduction in drinking with tone onset in Interval 20 in Condition 20(1)-30(6)-20(1) (line "a," Figure 11, top) replicates results from Experiment 2 in which drinking was suppressed in anticipation of upcoming food presentation. These data are additional evidence against explanations of schedule-induced drinking that rely upon post- or prefood factors.

EXPERIMENT 4
EFFECT OF FOOD MAGNITUDE ON DRINKING: FT 30

Few published studies of schedule-induced drinking have monitored drinking dynamics within sessions. Most studies report either session totals of drinking and bar pressing, or within-interval patterns. Perhaps the inconsistent results on the relation between food magnitude and level of drinking reflect changes in the relative levels of drinking and food-related activities across entire sessions; that is, over periods longer than the 30 FT 30-sec intervals studied in this experiment.

For example, in two sessions of equal duration, the one with more food per interval may satiate subjects faster than the one with less food. Drinking, then, might start at a higher level and decrease earlier in the session with more food per interval than it might in sessions with less food per interval. If so, the discrepancies between published studies regarding the effect of food magnitude on drinking might simply be due to the authors' choices of session length and food rate. It would not be surprising if in short sessions more food resulted in more drinking, but in very long sessions more food resulted in less drinking.

We examined this possibility by comparing drinking dynamics in sessions in which every interval ended in either one or six pellets with a FT 30-sec schedule (Experiment 4) or, a FT 120-sec schedule (Experiment 5). Since the results of the experiments replicate similar published work, they also serve to demonstrate that our other results are not attributable to differences between our apparatus and the conventional experimental chambers used in most other experiments on schedule-induced drinking.

METHOD

Subjects

The subjects were the same as in preceding experiments.

Apparatus

No modifications were made from Experiment 2.

Procedure

The four subjects were divided into two groups; in each group one subject had previous experience with the tone signaling extra food, the other the opposite. The tone was not used at all in this experiment. Group A (Rat B and Rat G) was exposed to a strictly alternating (daily) sequence of two session types: in Type (a), one pellet was delivered per interval; and in Type (b), six pellets were delivered per interval. Both session types had 40 intervals of

FT 30-sec per session. Group B (Rat F and Rat H) was exposed to a series of consecutive sessions of Type (a) followed by a series of Type (b). The results were the same for all animals, so it was unnecessary to recover Type (a) results in Group B.

Each subject was exposed to a minimum of 10 sessions of each condition after their drinking and eating patterns had stabilized. Supplemental food was given to each subject several hours after each session as necessary to maintain body weight at 80%, as in previous experiments.

Results and Discussion

Since the results from all subjects were similar, Figure 12 depicts the mean amount of drinking and food-related activity per interval across the sessions for all subjects and both food magnitudes. The heavy lines represent Type (a) sessions in which one pellet per interval was delivered, and the light lines represent Type (b) sessions in which six pellets per interval were delivered.

Drinking started at a higher level earlier in the six-pellet-per-interval sessions than in the one-pellet-per-interval sessions, but the effect is not large. For each rat, drinking declined more rapidly over the session with six pellets per interval than with one pellet per interval. There were no reliable differences between session totals of drinking with the two food magnitudes. Head-in-feeder was also higher early in six-pellet/interval sessions; it increased slowly across the session with both magnitudes.

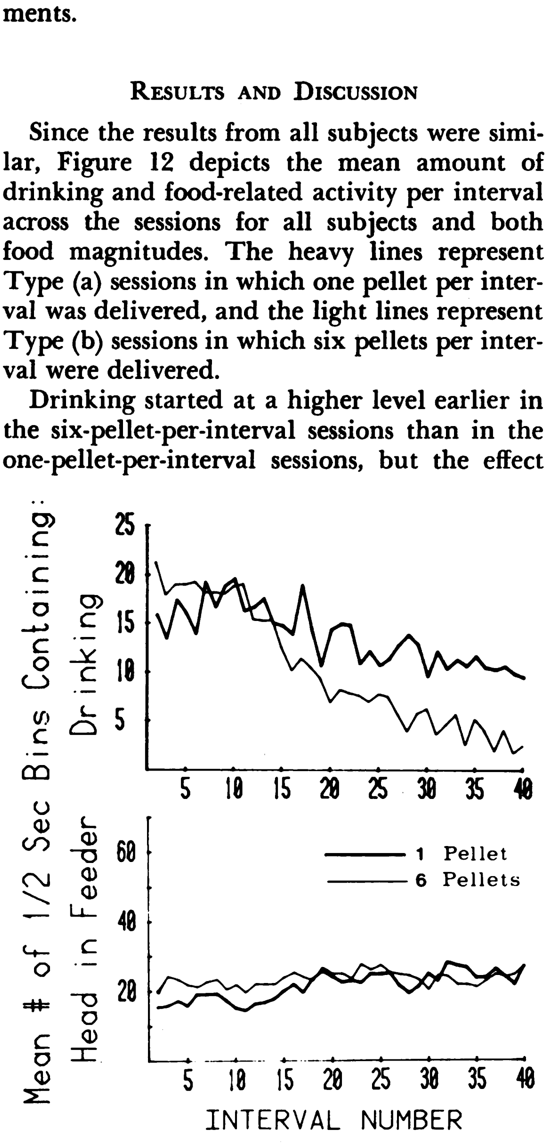

Fig. 12. Group mean number of ½-sec bins containing licking (top panel) and head-in-feeder (bottom panel) across one pellet per 30-sec interval (heavy line) and six pellets per 30-sec interval sessions (light line).

The point at which the drinking levels cross (the point which determines which magnitude induces more drinking when only session totals are used) may depend upon the interval duration, food magnitude, and perhaps the number of available activities. For example, six pellets per 30-sec interval might ensure greater competition between available activities for time than would fewer pellets delivered at the end of longer intervals. The last experiment looked at the effect of meal size on a FT 120-sec schedule.

EXPERIMENT 5
EFFECT OF FOOD MAGNITUDE ON DRINKING: FT 120

There was little difference between drinking levels early in the sessions in large- versus small-food-magnitude intervals in Experiment 4, but the small difference might be due to the fixed-interval being very short. The difference might be greater if the same number of pellets were delivered over longer intervals, thereby reducing the competition for time between available activities. In this experiment one or six pellets are delivered on a FT 120-sec schedule. As expected, subjects drank more with larger food deliveries for a larger proportion of the session than in Experiment 4.

Method

Subjects

The subjects were the same as in preceding experiments.

Apparatus

No modifications were made from Experiment 2.

Procedure

Two session types were used: Type (a) was 40 intervals of FT 120-sec with one pellet delivery per interval; Type (b) was 40 intervals of FT 120-sec with 6 pellet deliveries per interval, delivered 115 sec into the interval and spaced 1 sec apart. The four subjects were resegregated into two groups to control for possible effects of the procedure used in Experiment 4. Group A (Rat B and Rat E) was exposed to a consecutive series of Type (a) sessions followed by a series of Type (b) sessions. Group B (Rat G and Rat H) was exposed to a consecutive series of Type (b) sessions followed by a series of Type (a) sessions, thus controlling for the order of exposure to the two session types.

RESULTS AND DISCUSSION

As in Experiment 4, drinking started at a higher level early in the session and decreased more rapidly in sessions with six pellets per interval than with one pellet per interval (see Figure 13). The early differences in drinking levels between food magnitudes lasted over half the session (over 40 min), substantially more than in Experiment 4 (in which the entire session lasted only 20 min). Overall amount of drinking was clearly higher in the six-pellet condition at the 120-sec interval value. Head-in-feeder was consistently higher in the six pellets/interval condition and remained so throughout each session.

Since drinking starts at a higher level and decreases earlier in the session in sessions with six pellets per interval than in sessions with one pellet per interval, published results on the effects of food size on total amount of drinking presumably depend on both the interval value and the session length chosen. Our results resolve the inconsistency in the published studies, some of which show increases and others decreases in the total amount of drinking as food magnitude is increased. Session totals are not a useful measure of the effects of food magnitude.

The results from this experiment replicate published work showing that larger food deliveries can result in more schedule-induced drinking. Consequently, possible peculiarities of our apparatus can probably be ruled out as a reason for our failure to find either elicited or anticipatory drinking in the earlier experiments.

GENERAL DISCUSSION

These experiments show that although drinking in rats is augmented by certain periodic-food schedules, the direct relation between drinking and food-related behavior induced by individual pellet presentations is inhibitory rather than facilitatory: every manipulation that signaled an increase in the local probability of food presentation (e.g., a tone signaling a large upcoming meal or the previous presentation of a large meal) resulted in a decrease in drinking. The results provide no support for even a modest eliciting effect of food delivery on drinking. The experiments in which extra-food intervals were signaled also provide no support for the idea that stimuli associated with high food rates have a facilitating effect on drinking. Reid and Dale (in press) have confirmed both conclusions by observing eating-drinking dynamics within individual interpellet intervals when various signaled and unsignaled pellet magnitudes are delivered.

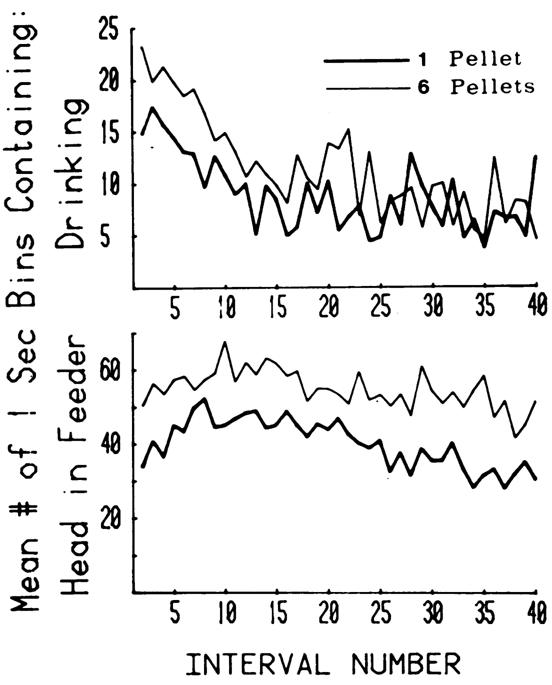

Fig. 13. Group mean number of 1-sec bins containing licking (top panel) and head-in-feeder (bottom panel) across one pellet per 120-sec interval (heavy line) and six pellets per 120-sec interval sessions (light line).

What then of results showing that drinking occurs less reliably after nonfood stimuli, even if they have exactly the same predictive significance as food (e.g., Alferink et al., 1980; Allen & Porter, 1977; Rosenblith, 1970)? The answer may lie simply in the poorer (temporal) discriminative control exerted by nonfood stimuli (cf. Staddon, 1974). When temporal control on periodic schedules is weak, the postevent pause is reduced, the time taken up by terminal responding increases—and the time available for interim activities such as drinking is reduced. Thus, it is not necessary to assume an eliciting effect of food on drinking to account for these results.

What of the results of Experiments 4 and 5 that do show a real, albeit transient, facilitating effect of large food magnitude on drinking? These results at least seem to imply a positive relation between signaled food rate and drinking. Yet our earlier results rule this out as a general conclusion. Experiment 2, for example, showed precisely the opposite: that a stimulus signaling a large increase in food rate suppresses drinking, although it facilitates food-related activities.

We are forced to conclude that the relation between the level of food-related activities and drinking is a nonmonotonic one: when the signaled meal size is very high or there is much competition from other activities, food-related activities increase at the expense of drinking, but when meal size is smaller, or there is weak competition from other activities, food-related activities and drinking may increase together. A similar, but more skewed, effect of meal frequency has long been known, of course (Roper, 1980; Staddon, 1977a): As food rate increases, food-related activities and drinking increase together; but at very high food rates, food-related activities continue to increase, but drinking rate decreases.

The precise mechanism for this nonmonotonic interaction is still elusive, but the obvious possibility is that it reflects two opposed processes. The process that produces an inverse relation between drinking and food-related activities is competition for available time, as we have demonstrated in these experiments (see also Reid & Dale, in press). The problem is to account for the opposite effect, a direct relation between the level of drinking and food-related activities. Our experiments rule out any direct effect of food on drinking; only indirect effects are possible. Perhaps the simplest indirect possibility is *disinhibition,* that is, an effect of food-related activities on drinking mediated by a third class of "other" activities (cf. McFarland, 1970).

It is easy to show that even if the direct effect of one activity on another is inhibitory, nevertheless, when there are three or more activities, an increase in one activity can be accompanied by an increase in another. For example, suppose that there are three classes of activity: x_1 (food-related activities), x_2 (drinking), and x_3 ("other" activities), and that activities are mutually inhibitory, as illustrated in Figure 14. The level of each activity is determined by two factors: its own causal (stimulus) factors—S_i in Figure 13—and inhibition from other activities that compete for the available time. For purposes of illustration, assume that these two factors are additive. Thus, the relation between any pair of activities can be represented by the linear equation

$$x_i = S_i - \sum_{j=1}^{3} a_{ij}x_j,\ j \neq i, \tag{1}$$

where coefficient a_{ij} represents the inhibitory effect of activity j on activity i, and S_i represents the causal factors for activity i (cf. Staddon, 1977b). Thus, the level of x_2 (drinking) in such a system is given by

$$x_2 = S_2 - a_{21}x_1 - a_{23}x_3. \tag{2}$$

Using the other two equations, x_3, the level of "other" activities, can be eliminated to yield

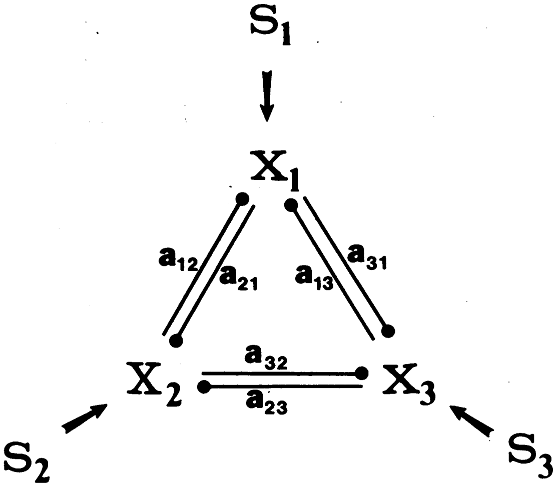

Fig. 14. Diagram of inhibition model. Arrows represent variable effects of exogenous and endogenous stimuli (*S*) on activities (*X*). Lines with filled circles represent the inhibition of one activity on another. Inhibitory strengths are described by the inhibitory coefficients (a), e.g., a_{12} represents the inhibition of x_1 by x_2.

the expected relation between x_2 and x_1, when only the causal factors for x_1 (i.e., S_1) are manipulated. This turns out to be

$$x_2 = [S_2 - a_{23}S_3 + x_1(a_{23}a_{31} - a_{21})]/(1 - a_{23}a_{32}). \tag{3}$$

Equation 3 has three interesting properties. First, if S_2 and S_3 are constant (i.e., the causal factors for drinking and "other" activities are constant), then the level of drinking is linearly related to the level of food-related activities with slope $(a_{23}a_{31} - a_{21})(1 - a_{23}a_{32})$. If (as we assume) the a_i are always less than unity the denominator is always positive. Hence this slope is positive if $a_{23}a_{31} > a_{21}$, that is, if the inhibitory effects of food-related activities on "other" activities and of "other" activities on drinking are both strong—but the inhibitory effect of food-related activities on drinking is relatively weak. Thus, given the proper quantitative inhibitory relations, an increase in food-related activities might be accompanied by an increase in drinking (as occurred in Experiments 4 and 5), even though the direct effect of food-related activities on drinking is suppressive.

A second property of Equation 3 is that the occurrence of drinking depends critically on the level of causal factors for "other" activities: if S_3 is high, the first term in the numerator is negative and may overpower the positive effect of disinhibition (the term in parentheses). Thus, the availability of a competing activity such as wheel running should reduce the level of schedule-induced drinking, as published results indicate (Staddon & Ayres, 1975)—although the positive relation between level of drinking and level of food-related activities should not be affected by the availability of a competing activity (cf. Staddon, 1977a). On the other hand, the causal factors for drinking (S_2) add in as a positive term, so that decreases in thirst (e.g., due to preloading with water) should reduce schedule-induced drinking, as several experiments have reported (Cope, Sanger, & Blackman, 1976; McFarland, 1970). If the inhibitory relations between activities are subject to a threshold, then if the causal factors for food-related activities are very large, all other effects are swamped and only food-related behavior can occur.

Finally, the sign of the relation between the level of drinking and the level of food-related activities depends in this model on the relative strengths of inhibitory relations among different activities. If these relations differ between species or individuals, both the type and level of schedule-associated behavior will differ accordingly. Thus, apparently qualitative differences may in fact reduce to quantitative differences in the strengths of built-in inhibitory relations.

Our results are not yet sufficient to confirm disinhibition as the mechanism underlying the increasing limb of the function relating schedule-induced drinking to food rate. The linear equations can only illustrate the possibilities: since the total function is bitonic, a complete model will be nonlinear (we hope to present a full account of such a model is the near future). And a static account, such as Equation 1, can only approximate the outcome of the dynamic interactions that must be involved. Nevertheless, disinhibition plus competition for time are processes sufficient to account for the known properties of schedule-induced drinking, and simpler, direct effects of food on drinking are ruled out by the present experiments.

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