1-1983

Dynamic effects of food magnitude on interim-terminal interaction

Alliston K. Reid

Robert H.I. Dale
Butler University, rdale@butler.edu

Follow this and additional works at: http://digitalcommons.butler.edu/facsch_papers

Part of the Behavior and Ethology Commons, and the Zoology Commons

Recommended Citation

This Article is brought to you for free and open access by the College of Liberal Arts & Sciences at Digital Commons @ Butler University. It has been accepted for inclusion in Scholarship and Professional Work - LAS by an authorized administrator of Digital Commons @ Butler University. For more information, please contact fgaede@butler.edu.
Dynamic effects of food magnitude on interim-terminal interaction

Alliston K. Reid and Robert H. I. Dale

Abstract

We tested the assumption of a facilitatory relation between periodic food presentation and schedule-induced drinking by examination of (a) elicited drinking, (b) drinking in anticipation of food delivery, and (c) possible indirect effects of food delivery on drinking. We exposed rats to a fixed-time 60-second schedule in which interfood intervals ended in either one or four food pellets with equal probability. In Phases 1 and 3, a stimulus signaled the magnitude of upcoming food presentation. In Phase 2, the stimulus was eliminated. Changes in drinking and "head-in-feeder" distributions within interfood intervals demonstrated that head-in-feeder was controlled directly by food presentation, but drinking was not. Head-in-feeder increased and drinking was reduced when large meals began or ended an interval. In Phases 4 to 6, meal size was manipulated across sessions yielding a positive relation between meal size and schedule-induced drinking. We conclude: (1) Schedule-induced drinking is determined by distributions of food-related behavior and results from indirect effects of food delivery; and (2) the amount of schedule-induced drinking and the form of the drinking distributions in this experiment can be accurately explained by two assumptions: (a) Food presentation facilitates food-related behavior through elicitation and anticipation; and (b) food-related behavior and drinking are reciprocally, linearly related.

Following Falk's (1961) demonstration of schedule-induced polydipsia in rats, several other schedule-induced activities have been obtained with various species, schedules, and reinforcers (cf. Falk, 1977; Staddon, 1977b). Most researchers have used schedule-induced drinking as a prototype, concentrating on the factors responsible for its excessive nature. Recently, increased attention has been directed toward the temporal distributions of induced behavior within interfood intervals on periodic schedules of reinforcement (e.g., Reberg, Mann, & Innis, 1977; Roper, 1978; see review in Staddon, 1977b).

Staddon's (1977b) model of schedule-induced behavior identifies three categories of behavior occurring on periodic reinforcement schedules: terminal activities, which occur in the presence of stimuli correlated with reinforcement delivery; interim activities, which occur in the presence of stimuli correlated with the absence of the scheduled reinforcer; and facultative activities usually occurring near the middle of interreinforcement intervals. An important distinction is that terminal activities are directed toward the acquisition of the reinforcer, whereas interim activities are not. Interim activities, including schedule-induced drinking, and terminal activities, including such responses as operant bar pressing and contacting the feeder, seem to be directly facilitated by schedule parameters that increase the rate of reinforcement and are, therefore, referred to as "induced" behavior. On the other hand, facultative behavior, such as wheel-running on certain
food-reinforcement schedules (Staddon, 1977b) is either reduced or unaffected by schedule manipulations that increase the rates of interim and terminal activities (Penney & Schull, 1977).

Several manipulations affecting food motivation appear to affect both interim and terminal (operant) behavior similarly. For example, the extensive literature on operant behavior suggests that operant behavior is directly controlled by several properties of reinforcement, such as reinforcement frequency (Herrnstein, 1961), reinforcement magnitude (Harzem, Lowe, & Davey, 1975; Harzem, Lowe, & Priddle-Higson, 1978), level of deprivation, and palatability of the reinforcer (Lowe, Davey, & Harzem, 1974). There appears to be a similar effect of these properties of reinforcement upon schedule-induced behavior (Bond, 1973; Cohen, 1975; Falk, 1972; Heyman & Bouzas, 1980; Wetherington, 1979; see review in Staddon, 1977b), although there is some question, discussed later, as to whether induced behavior is directly controlled by reinforcement. Because much of this evidence suggests a positive relation between food motivation and the rate of schedule-induced drinking, many researchers have come to the general conclusion that each interim activity is selected by a direct (causal) facilitory influence of the reinforcer on that interim activity. This facilitory relation is considered responsible for the excessive nature and the temporal location of the interim behavior (just after food delivery). In addition, the fact that only certain reinforcers have been found to induce interim behavior suggests that only those reinforcers have a facilitory relationship with the available interim behavior.

Even though interim and terminal behavior appear similarly affected by food motivation, food motivation may control the two classes of activities by different, distinguishable processes. The most obvious of these possibilities is that operant behavior is directly controlled by food presentation, whereas schedule-induced behavior is not controlled directly, but by the indirect action of food presentation on one or more other activities, particularly terminal activities, which in turn control interim behavior (McFarland, 1970; Reid & Staddon, 1982; Roper & Nieto, 1979; Staddon, 1977a, 1977b). In this case, interim behavior is only indirectly controlled by food presentation, and the temporal distribution of the induced behavior might result from some time-allocation strategy in which terminal behavior is more highly valued (Rachlin, Kagel & Battalio, 1980). The present study is designed to determine if the control of interim behavior by food presentation is indirect, and if so, to identify the intervening controlling responses.

If interim behavior does appear to be directly controlled by food presentation, the relation may or may not be facilitory. The relation does appear to be positive, however, and the present study directly tests the assumption of a facilitory relation between food presentation and schedule-induced drinking. This relation might be supported under either, or both, of two conditions.

(1). Drinking within an interfood interval may be controlled by prior food delivery. That is, drinking may be to some slight degree elicited by food presentation (Alferink, Bartness, & Harder, 1980; Allen & Porter, 1977; Rosenblith, 1970). Elicitation may simply refer to a positive relation between drinking and prior food presentation and need not refer to any strictly linear
relationship between food presentation and postprandial drinking as might be implied by a physiological interpretation.

(2). Drinking within an interfood interval may be controlled by stimuli, such as temporal cues, which signal upcoming food, and thus be in anticipation of food presentation (Fitzsimons & Le Magnen, 1969; Kissileff, 1969).

Experiments in which measurements are restricted to session totals of drinking and food-related behavior have been relatively unsuccessful thus far in the identification of the process(es) responsible for schedule-induction. Here, we present more detailed observations, i.e., the distributions of food-related behavior and drinking within interfood intervals, to depict the dynamic influence of food magnitude on both activities. A direct (causal) relation between eating motivation and amount of induced drinking requires both activities to vary proportionally with manipulations of food magnitude; and by manipulating prior or upcoming meal sizes, one can determine whether elicitation or anticipation is responsible for an apparent direct relation. If eating motivation and amount of drinking vary inversely (given published results that more food yields more drinking in between session comparisons), an indirect relation must be responsible.

Methods

Subjects
Four naive female rats (three albino rats reared in this lab approximately 5 months old and one Charles River hooded rat approximately 8 months old at the beginning of the study) were housed individually in one room with a 24-hr light cycle. One subject (Rat J) died between Phases 3 and 4. Their ad lib weights were determined 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 8 days. Water was freely available in the home cages.

Apparatus
The octagonal apparatus depicted in Figure 1 was used with all areas other than the feeding area, the center, and the area containing a retractable drinking tube blocked off. The distance between the feeder opening and the tip of the metal drinking tube was 66cm. The tip of the metal drinking tube was recessed .3 cm behind the clear Plexiglass wall, and all except the tip was electrically insulated. The contact-lickometer circuitry was designed by Allison 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 Formula M pellets 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 time of occurrence with 1/60 second resolution. These data were later transferred to diskettes for analysis.
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.

by PDP-11 minicomputer. Subjects were usually monitored informally via closed-circuit television.

Procedure
The four subjects were divided into two groups and were run seven days per week in six experimental phases of a fixed-time (FT) 60-sec schedule.

Phase 1. All 60-sec interfood intervals ended with approximately equal probability with either one or four food pellets. Subjects were run for 60 daily sessions on one of two conditions: For the two rats in Condition A, a tone-light combination was present during those 60-sec interfood intervals that ended in four pellets; for the other two rats in Condition B, the tone-light combination accompanied those intervals that ended in one pellet. For each condition, a session consisted of 48 intervals of a FT 60-sec schedule in which approximately half of the intervals ended in one pellet, and half ended in four pellets dispensed at 1/4-sec intervals.

This procedure yields four interfood-interval types, since intervals can begin with one or four pellets and can end with one or four pellets. Each of the four interval types occurred with approximately the same frequency (25%), and the random order was modified to ensure that the probability of one or four pellets following each meal was equal. Each subject was exposed to
two sequences of 48 food presentations, varied randomly across sessions to prevent subjects from learning a particular reinforcement sequence.

**Phase 2.** To distinguish the effects of the reinforcement preceding an interval (elicitation) from those of the reinforcement following the interval (anticipation), the stimulus signaling the magnitude of upcoming food was eliminated from the procedure described in Phase 1 by maintaining the stimulus combination constantly on for the two rats in Condition B and constantly off for the two in Condition A. Subjects were exposed to this procedure for 12 to 15 sessions.

**Phase 3.** This phase was a replication of Phase 1, in which the tone-light combination signaled the magnitude of the upcoming food presentation. Subjects were tested for 10 to 12 sessions.

**Phase 4.** All subjects were exposed to a FT 60-sec schedule in which one pellet was delivered at the end of every 60-sec interfood interval. All subjects received a minimum of 18 daily sessions, with 40 interfood intervals per session.

**Phase 5.** All subjects were exposed to a FT 60-sec schedule in which four pellets, dispersed every 1/4 sec, were presented at the end of each interval. All subjects received a minimum of 12 daily sessions, with 40 interfood intervals per session.

**Phase 6.** Phase 6 was a replication of Phase 4; each subject was exposed to 12 sessions.

In all phases, supplemental food (Purina Rat Chow) was given to each subject several hours after each session in order to maintain body weight at 80%.

**Results**

**Group Data**

Data are reported for the last eight sessions for each subject in each experiment phase. The group mean results, averaged across the four subjects, are shown in Figure 2; head-in-feeder is shown at the top of the figure, and drinking is shown at the bottom. The ordinate represents the mean percentage of 1-sec bins during the 60-sec interval for which the appropriate activity was observed.

During Phase 1, more time was spent with head-in-feeder during the first half of the interval when four pellets, rather than one pellet, began an interfood interval. The effect of the initial meal size (the meal beginning an interval) decreased as the interval progressed until the curves for intervals ending in the same meal size, the terminal meal (Interval Types 4-1 and 1-1, and Interval Types 1-4 and 4-4), converged at the end of the interfood interval. Head-in-feeder was facilitated by increasing either initial or terminal meal size.
The effect of meal size on drinking was strikingly different. The time spent drinking during an interval was reduced by increasing either initial or terminal meal size. In particular, there was far less drinking during Interval Type 4-4 ($\mu = 4.9$ sec/interval) than during Interval Type 1-1 ($\mu = 11.8$ sec/interval). Increasing initial meal size resulted in a temporal shift in the drinking distribution: Drinking occurred later in the interval after four pellets were delivered than after one pellet was delivered. The magnitude of the temporal shift was greater than that necessary for the consumption of the larger number of pellets (determined by visual observation and evident in Figure 2 by comparing the different rates at which the head-in-feeder distribution declined after large meal deliveries in Phases 1 and 5). For example, the distribution medians of Interval Types 4-1 and 1-1 differed by 20 seconds; Interval Type 1-1 peaked 28 seconds into the interval, whereas Interval Type 4-1 peaked only 12 seconds before the next pellet delivery. The onset of drinking after four pellets in Phase 5 (when four pellets were delivered ending every interval) occurred much earlier in the interval and was more abrupt than in those intervals in Phases 1 to 3 beginning with four pellets.

The Phase I results were replicated in Phase 3, with the exception that the total amount of drinking was reduced for all interval types. Of particular interest, there was still substantially more drinking during Interval Type 1-1 ($\mu = 8.9$ sec/interval) than during Interval Type 4-4 (3.2 sec/interval).

Fig. 2. Group mean percentage of 1-sec bins containing head-in-feeder (top) and drinking (bottom). Panels 1 to 3 represent Phases 1 to 3, and Panel 4 represents Phases 4, 5, and 6. In panels 1 to 3, the heavy solid line represents Interval Type 1-1; the light solid line, Type 1-4; the light dotted line, Type 4-1; and the heavy dotted line, Type 4-4. In Panel 4, the heavy line represents Phase 4 (1 pellet/interval); the dotted line, Phase 5 (4 pellets/interval); and the light solid line, Phase 6 (1 pellet/interval).
The differential effects of terminal meal size were eliminated in Phase 2, as expected, when the tone-light signal was removed (Figure 2, Phase 2). As in Phases 1 and 3, the time spent with head-in-feeder early in the interval was directly related to the size of the preceding meal. Late in the interval, when the effects of the terminal meal size had been dominant in Phases 1 and 3, time spent with head-in-feeder was the same for all interval types. Time spent drinking was not influenced by the terminal meal size and, as in Phases 1 and 3, drinking occurred later in the interval following four pellets than following one pellet. The time spent drinking was only slightly higher in Interval Type 1-1 (8.6 sec/interval) than in Interfood Type 4-4 (7.9 sec/interval). This suggests that the large effects of meal size observed in Phases 1 and 3 were mostly due to the stimulus combination signaling the meal size ending the interval.

A comparison of Interval Types 1-1 and 1-4 with Interval Types 4-1 and 4-4 in Phase 2 indicates that more time was spent drinking during intervals beginning with one pellet (9.0 sec/interval) than during intervals beginning with four pellets (7.9 sec/interval). This suggests that the large effects of meal size observed in Phases 1 and 3 were mostly due to the stimulus combination signaling the meal size ending the interval.

The head-in-feeder and drinking distributions for Phase 4 with one pellet per interval were not recaptured during the replication in Phase 6, suggesting a sequential effect of intervening Phase 5 (with four pellets per interval). Times spent drinking and with head-in-feeder were lower in Phase 6 than in Phase 4, but the shapes of the head-in-feeder and drinking distributions were similar in the two phases. The shift from one to four pellets per interval produced an increase in head-in-feeder early in the interval, with no change late in the interval (Figure 2, top, Phases 4 and 5). The return to one pellet per interval in Phase 6 resulted in a slight decrease in the amount of head-in-feeder early in the intervals with no change toward the end of the interval (Figure 2, Phases 5 and 6).
The effect of meal size on drinking was not consistent with the results of Phases 1 to 3: There was more drinking with it constant, although not explicitly signaled, four-pellet meal size (Phase 5, 10.0 sec/interval) than with a constant one-pellet meal size in either Phase 4 (9.0 sec/interval) or Phase 6 (6.5 sec/interval).

**Individual Subjects**

The group average data adequately reflect the manner in which meal size manipulations affected head-in-feeder and drinking for each of the subjects; that is, increasing the magnitude of food delivery beginning or ending a fixed interfood interval (when the latter was signaled) produced an increase in food-related behavior and a decrease in drinking. Moreover, the degree of control by the terminal meal size increased, and that of the initial meal size decreased, as a given interval type progressed.

The results for individual subjects are shown in Figures 3 to 6, and a comparison of the effects of meal size for the group and for individual subjects in each phase is made in Table 1. This table shows how increasing initial and terminal meal sizes in each phase of the experiment influenced the amount and distribution of drinking and head-in-feeder. The “amount” of each activity is the mean percentage of l-sec bins in the 60-sec interval during which the activity was observed; changes in the activity distributions could involve either changes in the shape of the distribution (roughly, the variance) or changes in its midpoint (roughly, its mean).

Table 1 shows that, with rare exceptions, all four subjects were similarly influenced by the manipulations of meal size. In Phases 1 and 3, increasing initial or terminal meal size generally increased the amount of head-in-feeder and decreased drinking (cf. Table 1; Figures 2 to 6).

![Fig. 4. Mean percentage of 1-sec bins containing head-in-feeder (top) and drinking (bottom) for Rat F, presented as in Figure 2.](image)
In Phase 2, increasing the initial meal size decreased drinking slightly for three of the four subjects, Rats D, F, & J (demonstrating that elicitation was only a minor effect of meal size), and increased head-in-feeder for all of the subjects, whereas varying the size of the (unsigned) terminal meal did not affect head-in-feeder.
Table 1. Effects of reinforcement-size manipulation on drinking and head-in-feeder: group mean and individual subject data.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Manipulation</th>
<th>Effect on HIF</th>
<th>Effect on Drinking</th>
<th>Displacement of Drinking Distribution</th>
<th>Displacement of HIF Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Subjects</td>
<td>D  F  I  J  Gp</td>
<td>D  F  I  J  Gp</td>
<td>D  F  I  J  Gp</td>
<td>D  F  I  J  Gp</td>
</tr>
<tr>
<td>I</td>
<td>Large</td>
<td>↑  ↑  ↑  ↑  ↑  ↓  ?  ↓  ↓  ↓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
</tr>
<tr>
<td></td>
<td>Preceding</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>↑  ↑  ↑  ↑  ↑  ↓  ↓  ↓  ↓  ↓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
</tr>
<tr>
<td></td>
<td>Following</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>Large</td>
<td>↑  ↑  ↑  ↑  ↑  ↓  ↓  ↓  ↓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
</tr>
<tr>
<td></td>
<td>Preceding</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>—  —  —  —  —  —  —  —  —  —  —</td>
<td>—  —  —  —  —</td>
<td>—  —  —  —  —</td>
<td>—  —  —  —  —</td>
</tr>
<tr>
<td></td>
<td>Following</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>Large</td>
<td>↑  ↑  ↑  ↑  ↑  ↓  ↓  ↓  ↓  ↓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  ✓</td>
</tr>
<tr>
<td></td>
<td>Preceding</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large</td>
<td>↑  ↑  —  ↑  ↑  ↓  ↓  ↓  ↓</td>
<td>—  —  ✓  ✓  ✓</td>
<td>✓  ✓  ✓  ✓  —</td>
<td>✓  ✓  ✓  ✓  —</td>
</tr>
<tr>
<td></td>
<td>Following</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meal Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

— Negligible changes, i.e., less than 10% in each observation.
? The two possible comparisons revealed opposite effects.

In Phases 4, 5, and 6, two of the three subjects systematically drank more when the meal size was four pellets than when it was one pellet, but the meal-size manipulation had no systematic effect on head-in-feeder.

Increasing initial meal size produced a predictable temporal shift in both the head-in-feeder and drinking distributions; these activities occurred relatively later after larger meals. However, the magnitude of both distribution shifts was greater than that necessary to eat the larger number of pellets (explained above). The influence of terminal meal size on the distributions was less reliable than the influence of prior meal size.

A strong negative correlation between the amounts of head-in-feeder and drinking was observed across most conditions and all subjects. The top graph in Figure 7 shows the relation of drinking to head-in-feeder obtained in Phase 1 (with all four interval types); data are presented for each interval type and each of the four subjects. A slope of -1 would represent the trivial situation of strict competition for time, but the observed slope of approximately -1/3 indicates that all
subjects made a trade-off of three sec of head-in-feeder for one sec of drinking (16 data points: four interval types with four subjects; \( r^2 = .89 \)). The group average is shown for each of the four interval types and is also closely fit by the same line. The results from Phase 3 (Figure 7, bottom; \( r^2 = .91 \)) closely replicate those of Phase 1.

**Discussion**

In Phases 1 to 3 all subjects increased terminal behavior (head-in-feeder) and decreased interim behavior (drinking) when four pellets, rather than one pellet, began or ended an interfood interval: The direct effect of increased food magnitude was to increase terminal behavior. If interim behavior is directly affected by reinforcement magnitude as many theories of schedule-induced behavior propose, drinking should have increased monotonically with terminal behavior; instead, the present results showed that drinking decreased monotonically as the level of terminal behavior increased.

**Fig. 7.** Mean drinking time (sec) versus mean head-in-feeder time (sec). Points represent the mean amount of time each subject spent engaged in drinking and head-in-feeder in each interval type in Phase 1 (Figure 7, top) and Phase 3 (Figure 7, bottom). Points representing group averages for each interval type are identified individually.
In Phases 11 to 6, when a constant amount of food was delivered after every interfood interval within a session, the sessions with the larger food magnitude resulted (for two of three subjects) in more schedule-induced drinking than the sessions with the smaller magnitude. This finding is important because it is consistent with an abundant literature based on experiments using the "standard" small operant chamber (e.g., Flory, 1971). We conclude that our observations in Phases 1 to 3 are not unique to our apparatus.

Since the direct, local effect of increased food magnitude on drinking within a session (in Phases 1 to 3) was to reduce drinking levels, we are forced to conclude that the dual effects of food magnitude on schedule-induced drinking result from direct (inhibitory) and indirect (facilitory) influences. This conclusion is supported by the results of Reid and Staddon (1982), which demonstrate direct inhibition of elicited and anticipatory drinking by food delivery.

Head-in-feeder is both elicited by food and occurs in anticipation of food delivery. As a glance at Figure 2 suggests, these effects are approximately additive. That is, the effect of an additional three pellets at the beginning or the end of the interval is approximately the same, no matter how many pellets occurred at the end or the beginning of the interval. For example, $F_{14}$ is approximately equal to $F_{11}$ plus the difference between $F_{44}$ and $F_{41}$.

These additive relations are most simply summarized by the following model:

$$F_{ij} = E_i + A_j$$ (1)

where all three terms are functions of postfood time and $F_{ij}$ is the distribution of head-in-feeder when the interval begins with $i$ pellets and ends with (signaled) $j$ pellets, $E_i$ is the hypothetical eliciting effect of the $i$ pellets at the beginning of the interval and $A_j$ is the hypothetical anticipatory effect of the $j$ pellets at the end of the interval. The model simply postulates that the observed head-in-feeder gradients are the results of a gradient of elicitation caused by pellets at the beginning of the interfood interval, plus a gradient of anticipation owing to signaled food pellets at the end of the interfood interval.

In the present experiment, $i$ and $j$ each take on two values, 1 and 4, yielding four empirical functions $F_{ij}$. By writing each of these as a function of the corresponding $E$ and $A$ gradients, we arrive at four simultaneous equations. By appropriate subtraction of pairs the following empirical relations can be derived:

$$F_{41} - F_{11} = F_{44} - F_{14}$$ (2)

and

$$F_{14} - F_{11} = F_{44} - F_{41}$$ (3)
Equation 2 summarizes the effects of elicitation because the anticipation effect (term $j$) is constant on both sides of the equation; similarly, Equation 3 summarizes the effects of anticipation because the elicitation term is constant. Both equations predict a linear relation, with unit slope and zero intercept, between the two difference distributions.

The corresponding empirical results (using the group data from Phase 1) are shown in Figure 8. The two panels depict the results of linear regressions on the difference distributions corresponding to Equations 2 and 3. A slope of 1.0 and an intercept of zero for both functions would confirm the additive model. The slopes of both lines are close to unity ($m = 1.17$ top panel; $m = .52$ bottom panel: both are close to unity since the range of possible slopes is from plus to minus infinity), and the intercepts are small, confirming the additive model as a reasonable summary of the effects of meal-size variation in this experiment. The wider range of data in the top panel (influence of elicitation, anticipation held constant) allows a much higher coefficient of determination ($r^2 = 97.7\%$) than in the bottom panel ($r^2 = 70.1\%$; influence of anticipation, elicitation held constant). As we have seen, the effects of elicitation on head-in-feeder are larger than the effects of anticipation in this experiment.

Thus, the probability that a rat will spend time with its head in the feeder opening depends upon the addition effects of elicitation and anticipation. We have also seen that there is a reciprocal relation between time spent at the feeder and time spent drinking (Figure 7). Moreover, the tradeoff favors head-in-feeder: A decrease of three seconds at the feeder yields an increment of only about a second in drinking. This is precisely what we would expect if time spent at the feeder is the major determiner of the amount and pattern of activity within each interfood interval: Three seconds of feeder time corresponds to only about one second of drinking because the other two seconds are shared among other activities. This argument has two implications: (1) Because drinking is linearly related to head-in-feeder, it should show the same kind of additivity as head-in-feeder (Equations 2 and 3); but the fit should not be as good, because these relations are derived from the relations for head-in-feeder, not directly; and (2) the temporal pattern of drinking should be predictable from the temporal pattern of head-in-feeder (this is just a restatement of the linear relation in Figure 7).

The first implication postulates that the observed drinking distributions are influenced by elicitation and anticipation; that is, both influences drinking levels. The following linear relations represent the additivity of the dual suppressive influences on drinking:

\[ D_{41} - D_{11} = D_{44} - D_{14} \]  \hspace{1cm} (4)

and

\[ D_{14} - D_{11} = D_{44} - D_{41} \]  \hspace{1cm} (5)
Equation 4 summarizes the suppressive effects of elicitation, with anticipation constant on both sides of the equation, and Equation 5 summarizes the suppressive effects of anticipation, with elicitation constant.

Using the group data from Phase 1, the two panels of Figure 9 depict the results of linear regression (as in Figure 8) in the difference distributions. Since the slopes of both lines are very close to unity (top panel, \( m = 1.05 \); bottom panel, \( m = .71 \)) and the intercepts are approximately zero, drinking shows the same kind of additivity as head-in-feeder. As expected, the fit of the linear regressions on these drinking data is not as good as the fit on the head-in-feeder data in Figure 8: The influence of elicitation, anticipation held constant (top panel), \( r^2 = 92.0\% \) (versus
97.7% with head-in-feeder); the influence of anticipation, elicitation held constant (bottom panel), $r^2 = 62.2\%$ (versus 70.1% with head in feeder).

The difference distributions for individual subjects of head-in-feeder and drinking are shown in Figures 10 and 11. Again we see that the effects of elicitation on head-in-feeder (top four panels in Figure 10) are more powerful than the effects of anticipation (bottom panels), evidenced by the wider range of points in the top panels than in the bottom panels. Since most points in each panel in Figure 10 lie in the first quadrant, increase in the size of initial or terminal meals yields increased head-in-feeder throughout the interfood interval for all subjects. Table 2 summarizes the $r^2$ values obtained from linear regresses of group and individual subject data for the effects of elicitation and anticipation on both head-in-feeder and drinking.

For all subjects, most points in the difference distributions of time spent drinking (Figure 11) lie in the third quadrant, indicating suppressive effects of increased initial or terminal meal sizes. Again, the effects of elicitation (top panels) on drinking are slightly larger than the effects of anticipation, evidenced by the wider range of points in the top panels than in the bottom panels.

We concluded that the drinking distributions are determined by the distributions of food-related behavior and inferred that the temporal pattern of drinking should be predictable by the temporal pattern of head-in-feeder. To predict the different drinking distributions, we must know something of the relationship between head-in-feeder and drinking. Figure 7 represents the linear
The solid line in Figure 12 summarizes the way in which the competition between drinking and head-in-feeder varied across the interfood interval. First, notice that all slope values are negative, demonstrating competition rather than facilitation throughout the interval. The slopes decrease

<table>
<thead>
<tr>
<th>Subject</th>
<th>Elicitation</th>
<th>Anticipation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HIF</td>
<td>Drink</td>
</tr>
<tr>
<td>D</td>
<td>94.3</td>
<td>71.1</td>
</tr>
<tr>
<td>F</td>
<td>36.5</td>
<td>59.5</td>
</tr>
<tr>
<td>I</td>
<td>71.0</td>
<td>60.8</td>
</tr>
<tr>
<td>J</td>
<td>95.1</td>
<td>94.0</td>
</tr>
<tr>
<td>Mean</td>
<td>74.2</td>
<td>71.4</td>
</tr>
<tr>
<td>Group</td>
<td>97.7</td>
<td>92.0</td>
</tr>
</tbody>
</table>
Fig. 12. Slopes and $r^2$ values obtained from linear regressions of time spent drinking and time with head-in-feeder within 6-sec bins across the 60-sec interfood interval. The figure represents group data obtained in Phase 1.

![Graph showing slopes and $r^2$ values over interfood interval](image)

Fig. 13. Predicted versus obtained drinking distributions for all four interval types. The obtained distributions in the top panel are copied from Figure 2 and are depicted for comparison to the predicted distributions. Predictions were based on Equation 6 with obtained head-in-feeder distributions.

![Graph showing predicted versus obtained drinking distributions](image)

throughout the interfood interval demonstrating that the temporal trade-off between head-in-feeder and drinking favors head-in-feeder less as the interval progresses. The decreasing trade-off by head-in-feeder implies that elicitation is a more powerful influence than anticipation upon
food related behavior. The $r^2$ values from each of the 10 regressions (depicted individually by “x”) were relatively constant over the interfood interval.

We are no in a position to explain how the different drinking distributions are determined by the head-in-feeder distributions. We can use the following equation to determine the influence of head-in-feeder on drinking:

$$D_{ij} = m F_{ij} + C_t$$

(6)

$D_{ij}$ and $F_{ij}$ represent the drinking and head-in-feeder distributions with initial meal size $i$ and terminal meal size $j$; $m$ represents the slope at time $t$ of the drinking/head-in-feeder function depicted in Figure 12, with drinking intercept $C$. 

The bottom panel in Figure 13 represents the predicted drinking distributions, and for comparison, the top panel depicts the obtained distributions from Phase 1 (copied from Figure 2). The predicted distributions were obtained by allowing each obtained head-in-feeder value (for each 1-sec bin in each interval type) to determine the degree of suppression of drinking below the drinking intercept $C$ (at time $t$) according to Equation 6. The degree of suppression varied across the interfood interval as the slope (from Figure 12) and intercept varied. Comparison between panels shows that the shapes and absolute magnitudes of all four distributions are accurately predicted. The accuracy of each prediction is strong evidence that drinking distributions are simple, indirect functions of elicitation and anticipation, even though the reciprocal relation between food-related behavior and drinking is not linear across the interfood interval.

Thus, the amount of schedule-induced drinking and the forms of the drinking distributions within the interfood interval in this experiment can be accurately explained by two assumptions: (1) Food presentation facilitates food-related behavior through elicitation and anticipation; and (2) food-related behavior and drinking are reciprocally, linearly related.

References


