Feeding patterns in rats on restricted access schedules: Palatability, bulk, and other determinants of intake

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Rats were adapted to 2 h or 4 h restricted daily feeding schedules. The feeding patterns were continuously recorded using a strain gauge. Different groups received different powdered foods, and some groups were switched to different diets at a late stage of adaptation to the original diet. Feeding behavior became continuous throughout a 4-h access when a cellulose diluted diet was presented. In contrast, calorically denser diets were taken in two or three discrete meals during the session. Bitter foods were eaten slowly. The results show that a consideration of different momentary feeding patterns can give more useful insights than a simple measure of the total amount ingested during the session. It is suggested that oral satiety factors or mechanical constraints may pose an upper limit when feeding calorically diluted diets, while postingestive events may limit the intake of denser diets. Liquid diets may be subject to still different constraints.

The degree of hunger of an organism is typically assessed through a measure of the amount of food ingested in a fixed time, or by the amount of work the animal will perform to obtain food. Studies using the former restricted feeding schedule (e.g., 1 or 2 h access per 24 h) have devoted little attention to the feeding behavior itself. Amount ingested is the time integral of the momentary feeding rate (FR). If a particular manipulation leads to a decreased FR, then the session may end before spontaneous cessation of feeding would have occurred. In this case, the lowered intake need not necessarily reflect diminished "hunger"—but be secondary to the cause of the lowered FR. The analysis of meal patterns in freely feeding rats has led to considerable advances in our understanding of the substrates for eating behavior (LeMagnen, Devos, Gaudilliere, Louis-Sylvestre, & Tallon, 1973). Relatively little attention has been paid to events occurring within brief access times (Ghent, 1957; LeMagnen, 1967; Skinner, 1930; Smith & Duffy, 1957). In particular, no systematic study of possible interactions between access time, palatability, caloric density, and adaptation to the schedule, has been performed. The present work is a preliminary approach to some of these interactions, using within-session records of feeding as dependent variable.

METHOD

Male Wistar rats weighing about 300 g at the start of the experiment were individually housed with lights on 0730-1930 h during several days' adaptation with food and water available ad lib. The baseline 24-h intake of lab chow

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(Extralabo M25 poudre, 3.2 kcal/g) and bodyweight (BW) were recorded at this time. The 18 rats were then divided into five groups and food deprived 20 h before the start of their first scheduled experimental feed. Thereafter food was never available in the home cage. The experimental phase (up to 20 days) consisted of a 2 or 4 h per day food access, at the same hour (daytime) according to the group assigned. The feeding cage, in an adjacent lighted room, was fitted with a continuously weighing food cup (strain gauge), and the dc signal was appropriately transduced to a chart trace. Water was available in the feeding cage, and in the home cage. The five experimental groups were: 4C-4-h presentation of standard powdered chow (C), $N = 4$; 4D-4-h cellulose diluted diet (D), $N = 4$; 4Q-4-h quinine adulterated chow (Q), $N = 4$; 2C-2-h diet C, $N = 3$; 2S-2-h saccharin sweetened chow (S), $N = 3$.

After varying periods of exposure to the original diet, selected groups were shifted to new diets; these are appropriately abbreviated in the results. The diets were designed to be comparable with those used by Booth (1972). Diet S was chow with 0.05% Na saccharin added; Diet Q was chow plus 0.5% quinine hydrochloride. Diet D consisted of (w/w) 50% chow, 40% cellulose flour, 10% Kaolin with 0.75% Na saccharin. The caloric value (based on nonutilizable cellulose) is 1.6 kcal/g, and the bulk density 0.6 g/ml ($C = 2$ g/ml). D is not too unpalatable from the human tastepoint, but is dry and "powdery" and subject to much spillage, allowed for in all calculations. Unless otherwise indicated, all rats within a group showed very similar behavior, and group means are indicated in the results.

RESULTS

Group 4C

This group required an adaptation period of about 3 days, after which time daily intakes were stable at 13 g and BW at 28 g below initial level. (The preexperimental ad-lib food intake was 21-24 g/24 h, with average BW gain of 2.0 g/day). Figure 1 presents the cumulative intake records for different days on experiment. The amount eaten in the first hour increased across days ($p < .05$), but the intakes in following hours did not show a similar statistically significant trend. The animals tended to eat two major "meals" in the time available; this is reflected in the high intake in the first hour

Figure 1. Patterns for rats with 4 h per day food access. Left: Hourly cumulative food intakes for Group 4C. The figures at the right indicate the day of experiment. M is the mean curve for Days 3-9 feeding Diet C. During this time, the individual patterns of feeding were unchanged and similar for all animals, although the amount taken in the first hour increased in a linear ($p < .05$) way across Days 1-10. D is the mean intake curve for Days 10-16, when the rats were switched to Diet D (cellulose diluted). Curve C is the mean for Days 17-19 when refed chow. $N = 4$.

Right: Similarly for Group 4D eating Diet D Days 1-14 (M is mean curve for Days 2-13). The total (4 h) intake increased as a linear function of days on schedule ($p < .01$), while it is evident that the majority of the increased intake after Day 4 occurred in the latter stages of the session. Note the smooth, negatively accelerated curves M, & Days 12 and 13, representative of all rats. When switched to Diet C (Days 14-17) there is a marked inflection of Curve C, reflecting a midsession pause in feeding.

(greater than in any other hour, $p < .001$), and in the third hour (intake greater than in Hours 2 and 4, $p < .05$). However, the size of the second meal did not increase across days. The patterns of feeding of individual rats were stable after Day 3. The FR during the first hour was negatively accelerated (Table 1) which confirms earlier studies using 1-h sessions (Skinner, 1930; Smith & Duffy, 1957). Observation of the animals suggested that this effect was due principally to the more frequent occurrence of short pauses for drinking and grooming, rather than changes in within-bout FR. On Day 10, Group 4C was switched to Diet D. The daily intake fell temporarily, and then increased over the next 6 days to 19 g/session. During this time, BW loss was precipitous (> 5 g/day). The cumulative feeding record underwent considerable change, with the appearance of a smooth, negatively accelerated intake throughout the session (Figure 1 and Table 1) with no evidence of pausing for more than 1-2 min at a time.

Group 4D

This group took considerably longer to adapt to diet and schedule than Group 4C. At first, the gram intake of D was actually less than the intake of C by Group 4C. However, intake continued to rise slowly with days ($p < .01$, Figure 1), and by Day 13 the 4-h intake was 20 g (but only 32 kcal—still less than Group 4C on Diet C). BW fell by a mean of 70 g during this time. It may be seen from Figure 1 that the increase in intake between Days 4 and 9 was achieved by the incidence and then the persistence of feeding in Hours 3 and 4. Individual records showed that the pattern of discrete bouts and pauses seen up to Day 8 had been replaced by continuous eating throughout the 4 h, with pauses only for drinking.

Groups 2S and 2C

As for 4-h presentations, animals of the 2-h groups showed daily increases in intake correlated with adaptation time ($p < .01$). By Day 7, the intakes were stable at about 14 g for both C and S diets. Table 1 shows that the FR increased through Day 4, and thereafter the total time spent eating was also increased. The pattern of intake evolved to one of a large initial bout, a short rest, and a second bout which lasted until the end of the session. The FR on Diet S was greater than C (Table 1), while the total eating time was less on Diet S, hence intakes were about equal.

Group 4Q

All of the animals showed low intakes of 5 g or less

Table 1
Averaged Feeding Rate Data

Diet	Group	Day 2		Stable		Final	
		30 mn	1 h	30 mn	1 h	30 mn	1 h
C	2C	8.8	7.4	10.8	8.8	13.2	12.8
	4C	4.7	4.8	8.5	5.8	9.8	8.4
	4D					13.2	10.6
	4Q					11.6	8.6
S	2S	6.8	5.8	10.6	8.7	11.7	10.1
	4Q	4.8	3.8	5.9	4.7		
D	4D	6.0	4.4	10.2	8.8		
	4C			6.5	6.0		
	2S			10.7	8.4		

Note—Group mean food intakes (grams/hour) of diet shown are tabulated for measures at 30 min and 1 h into the access period. Values are given for Day 2, on a day after considerable habituation (stable: range Days 8-14 depending on group), and in a final stage when eating regular Diet C (except Group 2S eating S).

during the first 4 days. Feeding was intermittent, and FR lower than for other diets. Two of the rats maintained this pattern of slow, long bouts (Table 1), and long pauses, throughout the experimental period. The other two rats showed a sudden increase of intake at about Day 5, and this was achieved almost exclusively through an increase of FR within bouts, rather than by an increase in time spent feeding. The FR, in fact, approached that of rats eating C. Indeed, on Day 14 when the animals were switched to unadulterated Diet C, the two "rapid" eaters showed little change in their 4-h intake, while the two "slow" eaters showed an immediate doubling of intake (8 to 16 g). The FR changes again mediate these effects (Table 1).

DISCUSSION

Feeding behavior is under multiple factor control, and it is thus difficult to design experiments which isolate the effects of experience, taste, BW level, caloric density. The present experiments have attempted a partial factorization, and some initial conclusions may be drawn.

Caloric density and bulk seem to be important limiting factors under the restricted access paradigm. Rats on a 2-h/day schedule have difficulty in adapting to a dilute diet (Smith, Pool, & Weinberg, 1961), and these authors suggested that bulk in the stomach could be a principal inhibitor of intake. However, the present analysis suggests that an alternative or complementary explanation should include oral factors—specifically the animals cannot chew and swallow more bulk in the time available. This is demonstrated by the continuous feeding patterns of Group 4D. In support of the oral limit idea, only extremely large gastric preloads of nonnutritive bulk were found to suppress subsequent intake during a scheduled feed (Smith & Duffy, 1957). At the oral level, the bulk measure kcal/ml, is likely to be a critical property. By inference, rats eating Diet C could have handled more bulk at the oral level, so gastric distention and/or

postabsorptive factors presumably intervene to generate the "feed and pause" pattern. Against the oral limit notion, Young, Gibbs, Antin, Holt, & Smith (1974) have observed extremely large intakes of a liquid diet, when that diet is immediately drained from the stomach. However, there are probably very different mechanical constraints on liquid vs. solid food at the oral level, as well as systemically.

Palatability seemed to be reflected in FR with the highest rates on Diet S. However, it is interesting that the "slow" Q eaters continued to show long pauses during the session, rather than coming to eat slowly and more or less continuously throughout the 4 h. The rats which did ingest more Q did so by increasing FR. It is not clear whether this difference might be reflected in other traditional measures of aversion such as taste thresholds.

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