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Effects of meal frequency and snacking on food demand in mice

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Abstract

Ad libitum feeding patterns in mice show substantial differences between laboratories, in addition to large individual and time-of-day differences. In the present study, we examine how mice work for food when access to food is temporally restricted and so they are forced to take discrete meals. In a first experiment, separate groups of ICR:CD1 mice were given access to food for 4, 8 or 16 opportunities or meals per day, with the duration of access at each opportunity adjusted reciprocally so that the total time of availability was 160 min per day in all three conditions. During the periods of availability, mice were able to earn food pellets by nose poke responses, according to an incrementing series of fixed unit prices (FUP: 2,5,10,25) with each schedule in force for 3–4 days. Total food intake was similar in all three groups, indicating that mice generally were able to adjust their intake to a range of temporal availabilities. In each group, food demand fell as FUP increased. In the 8 and 16 meal groups, no food was eaten in many of the opportunities. Within an opportunity, the rate of intake generally declined with time, indicative of satiation. At low FUPs, later opportunities in each day were associated with smaller meals than earlier opportunities; in contrast, at high FUPs the first opportunity was also a small meal. Collectively, these results show that mice eat less at higher costs but not because of time constraints of the schedule: instead, they exhibit an elective anorexia. In the second experiment, we examined whether snacking between imposed meals would affect subsequent meal(s). Mice were adapted to the foregoing 8 opportunity protocol. Then, half the mice received free snacks of sugar cubes after the 3rd, 4th and 5th meal opportunities and the intakes of sugar and pellets were examined at low and high unit costs for pellets (FUP 2 and 25). At FUP2, mice decreased demand for pellets and compensated energetically for the sugar they consumed. At FUP25, mice also decreased demand, but by less than the energy obtained from sugar. These data show that choice for pellets over a free palatable snack, and subsequent compensation of energy intake, is modified by effort and demand.

Introduction

Obesity has become a leading cause of morbidity and mortality throughout the world (World Health Organization, 2005). Physiological factors alone are unable to account for increased incidence of obesity. For example, when the timing and amount of food consumed is examined relative to actual energy deficit, the impulse for starting a meal is not always based on a physiological deficit. Instead, the initiation of a meal may be based mostly on factors such as social and/or habitual patterns, convenience, or time of day (Woods, 2005). In particular, people who habitually eat snacks between meals have increased body mass

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index (McCrory, Suen & Roberts, 2002). In contrast, other reports suggest that large meals and/or low frequency of feeding leads to more efficient energy utilization than a high frequency of feeding, also known as grazing (Fabry et al., 1966; Kanarek, 1997; Parks & McCrory, 2005). Given the apparent and procedural differences among these human studies, we developed a protocol to investigate whether mice can adjust their total daily intake to different experimentally-imposed meal frequencies. Our previous studies in mice have found substantial individual variation in meal parameters (Chaney & Rowland 2008); many mice seem to take some prolonged but slow meals, or apparent grazing, especially at night. One purpose of the present experiments is to examine the adaptation of mice to what amounts to an imposed meal pattern. In addition we examined whether mice that receive snacks between these imposed meals adjust subsequent meal sizes and/or total intakes. This protocol is modeled after a study in rats using free sucrose solution (Lea & Roper, 1977).

In previous work, we have reported closed-economy food demand functions for mice under a variety of conditions in which they emit behavioral responses to obtain food pellets (Atalayer & Rowland 2009; Chaney & Rowland 2008). In those studies, we have found that when work is imposed as an inescapable fixed unit price (FUP), total food intake declines at relatively high unit prices (eg 50-100 responses per 20 mg pellet), but that the meal pattern remains relatively constant despite the fact that inter-pellet intervals and meals become extended in time as FUP increases. In contrast, when an access cost followed by the unit price is imposed, mice tend to minimize their effort by taking fewer but larger meals (Atalayer & Rowland, 2009; Chaney & Rowland, 2008; Vaughan & Rowland, 2003). Thus, as was first suggested in rats by Collier, Hirsch & Hamlin (1972), meal patterns are determined primarily by the economy in which food is available. Thus, another purpose of the present studies to examine adaptation of meal size to changes in unit price when meal frequency is experimentally imposed.

Methods

Subjects and housing

A total of 31 male albino mice (ICR:CD1; Harlan, Indianapolis IN) initially about 2-3 mo old were used in the protocols. This strain was chosen because they are of mixed origin and have food intake near the middle of a range of strains of mice (Bachmanov et al., 2002). All animal use in this experiment was approved by the Institutional Animal Care and Use Committee. For 1-2 weeks between receipt and the start of the experiments, mice were housed individually in polycarbonate cages with Purina 5001 chow pellets and tap water available ad libitum. The vivarium was temperature ($23\pm2^{\circ}\text{C}$) and humidity (40-70%) controlled, with a 12:12 light cycle (lights on 0500). During the experiments, mice lived in test chambers for 23 h/day. Mice were weighed daily and transferred to holding cages without food during a 1 h cleaning period during the middle part of the day. During 23 h test sessions, mice obtained 20 mg nutritionally-complete pellets (Purina Test Diet 5TUM, a grain-based tablet with 10.4% kcal from fat and 24.1% from protein) when they completed a price determined by the particular reinforcement schedule.

Operant behavior chambers and general procedure

Testing occurred in 24 behavior test chambers (Med Associates, St. Albans, VT: 13×13×12 cm), with Plexiglas and alloy walls and stainless steel grill floor. Each was contained within a ventilated, noise attenuating cabinet with the same 12:12 light cycle (lights on 0500) as the vivarium via a 7 w bulb in a night light fixture run from a 24 h timer. Chambers were equipped with a nose poke device with a small cue light above. The device was located 2 cm above the floor and adjacent to a food receptacle. Water was supplied freely from sipper tubes mounted on the wall opposite the food receptacle. A record of total pellets obtained

and number of nose poke responses were acquired by MED-PC IV computer software (Med Associates). Data were accumulated in 5 min time bins throughout each session.

Experiment 1: effects of feeding opportunity frequency on food demand in mice

A total of 15 mice were divided into 3 imposed meal frequency groups, matched for initial body weight. As described above, mice lived in the behavior chambers for 23 h/day, but food was only available for 16 h corresponding to the 12 night hours and 4 h of the next day. To habituate mice to the chambers and the 16 h availability of food, a training protocol was used with a FUP2 schedule in which a food pellet was delivered after every 2 nose poke responses. Mice were deemed to have learned this task when they earned enough pellets over 16 h to maintain their body weight.

During the main procedure, the first group had access to food for 10 min at the beginning of every hour, so received 16 feeding opportunities and a total of 160 min access per day. The second group had access to food for 20 min at the beginning of every second hour, so received 8 feeding opportunities and a total of 160 min access per day. The third group has access to food for 40 min at the beginning of every fourth hour, so received 4 feeding opportunities and a total of 160 min access per day. Food pellets were contingent upon the completion of the operant responses as determined by the FUP schedule (2, 5, 10, and 25 responses per pellet). Based on our previous work, it was planned that each schedule would be in force for 4 days but the FUP25 phase was truncated at 3 days due to unexpectedly high weight loss.

Experiment 2: effects of snacking on food demand

A total of 16 naïve mice were divided into two groups matched for initial body weight. Nose poke training was applied as in Experiment 1. The first group (control) was studied during a 10 day adaptation to FUP2 for 20-mg food pellets (only the last 2 days were used to compute baseline data), during a 3 day period of FUP25, and then during return to FUP2. The second group (snack) was presented additionally with sugar cubes (Domino sugar cubes, ~2.5 g or 10 kcal per cube) for 20 min three times a day, placed on the grill floor inside the chambers. These presentations were for 15 min and occurred during the dark cycle exactly 30 minutes after the 3rd, 4th and 5th feeding opportunities. The sugar cubes were weighed before and after each presentation and a new sugar cube was presented each time. The doors of the operant chambers of the control mice were also opened and closed at the same times. Any spillage was counted daily and subtracted from the data each day. Food pellets were contingent upon the completion of the operant responses as determined by the FUP schedule (2 or 25 responses per pellet). Based on our previous work, it was planned that each schedule would be in force for 4 days but, as will be noted in the results, the last phase was truncated due to weight loss, and one mouse was removed from the study.

Data analysis

The number of responses emitted during each feeding opportunity and the number of pellets earned were recorded to a resolution of 5 min, although only total responses and pellets per opportunity were used for analysis. Spilled pellets found beneath the cage floor were subtracted from the total earned; in every case spillage was small (typically <5% of the number earned). Non-eating episodes were defined as opportunities with <2 pellets received (most were 0). For each mouse, data were averaged across the last 2 days of each cost or reinforcement schedule. These data were then treated using ANOVA and post hoc Newman-Keuls tests to assess specific differences; in all cases, $P < 0.05$ was considered significant.

Results

Experiment 1: effects of feeding opportunity frequency on food demand in mice—The demand functions for the 4, 8 and 16 opportunity groups are shown in Figure 1, panel A. Daily intake declined as unit price increased, but all three groups showed similar effects. Thus, two-way ANOVA with groups and price as main factors was significant ($P < 0.001$), with a main effect of price ($P < 0.001$), but no significant effect of group or group $\times$ price interaction. Mice lost body weight as the FUP series incremented (Figure 1, panel B), in particular at FUP 25 when intake was lowest. Thus, food demand was insufficient to maintain body weight. There was marked individual variability in weight loss (and corresponding intake) at higher FUPs, and one mouse in the 4 opportunity group was removed from the FUP25 phase of the study due to cessation of food intake and excessive weight loss.

Meal-by-meal effects were examined, and the data have been reduced for presentation in Figure 2. Data for the 8 and 16 opportunity groups were collapsed into four 4-h time bins equal to the intermeal intervals in the 4 opportunity group: thus, for the 8 opportunity group meals 1-2, 3-4, etc were combined, and for the 16 opportunity group meals 1-4, 5-8, etc were combined. In addition to showing that intake declined as FUP increased, it may be seen that at FUP2 and 5 intake declined as the 16 h daily feeding window progressed and in particular in the last 4 h. In contrast, at FUP 10 and 25, intake in the first 4 h was lower than in hours 5-12. A sharp decline in the intake during the last 4 h occurred despite the fact that at higher costs the total daily intake was low and mice were losing body weight.

The distributions of meal size are shown in Figure 3. Not surprisingly, larger meals occurred at the lower FUPs and smallest number of imposed meals. However, an unexpected feature was that in the 16 meal group, about half of all meal opportunities contained no eating. Examination of individual data (not shown) indicated a tendency toward alternation, viz a meal followed by a zero meal. In the 8 meal group, about 35% of all opportunities were likewise missed, while at 4 meals the number of missed meals was ~20% overall but was notably larger at high (~30%) than at low (~10%) FUP.

The mean feeding rate within meals for the 4 opportunity group is shown in Figure 4. In general, the number of pellets taken declined in successive 5 min time bins during the 40 min window of opportunity. At all FUPs, meal 2 showed the highest or near-highest feeding rates, and in general these correlated with the total meal sizes that were shown in Figure 2. Note however, that at all FUPs and in particular at FUP25, one or more of the meals—often the last—was associated with a low average initial rate of feeding, although this was related to the number of zero meals that were averaged into this number (cf Figure 3). Data were generally similar for the 8 opportunity group (not shown). In the 16 opportunity group, mice consumed more in either the first or second 5 min half of each meal, but with no consistent pattern.

Experiment 2: effects of snacking on food demand—Figure 5 shows the total intake in both groups during the three phases of the study. Two way ANOVA for pellet intake was significant ($P < 0.001$) with main effects of the phase of group ($P < 0.001$) and phase of the study ($P < 0.001$), but no interaction. The intake during the FUP25 phase was significantly lower than in either of the FUP2 phases. Total energy intake of the snacking group did not differ from non-snackers in the FUP2 phases because their reduction in pellet intake was precisely offset by their intake of sugar. In the FUP25 phase, the snacking group ate more sugar than during the FUP2 phase, and their total intake was higher than in non-snackers. As a result, the snacking group lost less body weight (-1.0 ± 0.3 g) than non-snackers (-2.5 ± 0.6 g, $P < 0.05$) during the 3 days of the FUP25 schedule; all mice regained the lost weight during the subsequent 3 days at FUP2.

The size of the individual meals is shown in Table 1, along with the % of feeding opportunities in which >1 pellet was obtained. Sugar was eaten at every presentation. Overall, non-snacker mice ate pellets in 70% of available intervals and snacking mice ate in 64% of available intervals.

Discussion

Our previous studies on food demand in mice have shown that they spontaneously eat ~15 meals per day (depending on the meal-defining criterion), mostly at night, with a mean size of ~15 pellets (Atalayer and Rowland, 2009). As unit price increased, meal size declined slightly. However, under both low and high cost conditions, some meals occurred over quite long periods of time (grazing). We thus examined whether mice would adapt to various imposed regimens of food availability that would, in effect, force faster or more sustained eating episodes. While mice adapted to the imposed schedules, including not taking advantage of all opportunities (Fig 3) they showed markedly greater elasticity of demand than in our previous continuous access studies. For example, with 23 h/day uninterrupted access (Atalayer & Rowland 2009), demand functions did not decline significantly until FUP50, then only by ~20% from demand at FUP5. In contrast, in the present work, intake was reduced by >50% at FUP25 (Fig 1A), and we were unable to progress to a planned FUP50 phase.

There is, it might be argued, a trivial reason for this – that 160 min was insufficient time to complete the required responses and consume the food (with the exception of FUP2 in a few mice, we do not find food accumulation in the food receptacle). However, our data argue against this possibility. To obtain free feeding levels of food intake (~250 pellets or 5 g per day), mice would have to sustain an average inter-pellet interval of about 38 sec (8 pellets/5 minute bin) throughout the 160 min access. At all FUPs, maximum group mean rates (including averaged zeros) reached or exceeded 8 pellets/5 min (Fig 4). Further, if we take the group maxima from any 5 min bin (Fig 4) and assume these reflect completely uninterrupted feeding - consisting of nose poke response time plus handling time (retrieve, chew and swallow the pellet), we can solve simultaneous equations to obtain independent values for response and handling times. Solving for FUP2 and FUP5 yields response time = 0.65 s and handling time = 11 s. Substituting these values for FUP10 yields a close fit to the observed data. However, for FUP25, these values would allow a maximum pellet yield of 11 per 5 min, considerably more than the maximum (8) mean observed. Thus, we can conclude that at FUP25, despite the fact that intake has dropped to 50% of control levels and substantial weight loss occurs (Fig 1), we can conclude that mice are maintaining responding well below theoretical maxima. That is, their anorexia is “elective” rather than forced by the absolute constraints of the schedule. This may be due to three factors: individual variation in response and handling times, interruption of pellet-directed activity and/or submaximal response rates, and the general increase in this latter factor and so a lower local feeding rate as a meal progresses (Fig 4). As a representative example of individual variability from the 8 opportunity group, the individual 2 day mean intakes at FUP 2 ranged from 224 to 324 pellets ($\pm 18\%$ of the mean) whereas at FUP 25 the range was 45-214 ($\pm 64\%$ of the mean). As a result, some mice maintained intake and thus body weight reasonably well at high FUP while others did not. However, even the best responders did not show maximum rates in all of the intervals. Thus, factors other than or in addition to ratio strain must be producing the high elasticity of demand in this protocol. We did not collect data with a resolution less than 5 min, but this will be necessary to address the contributions of interruption and local response rate to overall demand.

In addition to the “elective” interpretation of low demand at high FUP, another surprising result was the fact that given 16 opportunities to eat, only half were taken. Instead, the mice squeezed their intake into ~8 intervals. The 16 opportunity group was designed specifically

to emulate a criterion-derived ad lib meal frequency and circadian distribution (Atalayer and Rowland, 2009). If low intake and weight loss, and/or ratio strain, were limiting factors, then animals would have been expected to take advantage of all opportunities. They did not, and this was especially remarkable at FUP25 when most animals were losing considerable weight. Interestingly, the number of feeding opportunities did not have an overall effect on food demand (Fig 1A). As the imposed schedule deviated further from an ad lib-like pattern, mice seemed well able to adapt to this change. This makes their inability to respond optimally to each of the opportunities all the more puzzling.

The data show evidence of within-meal (Fig 4) as well as across-meal (Fig 2) satiation, characterized at least in some cases by increased interruption of food-directed behavior. The generally similar shapes of the within-meal satiation functions for a given meal (Fig 4) despite markedly different total intakes in those meals suggests that time as much as amount consumed is contributing to these effects. This makes ecological sense for a prey species – the longer they are sustained at a task the higher their likelihood of predation and hence a need for increased interruption, perhaps to attend to potential non-food stimuli. Of course, we are using laboratory bred mice with no apparent distractions but the hypothesis could be tested by adding subtle distractions. Changes in mean meal sizes across the opportunities within a day (Fig 2) show that intake is not consistently highest at the first meal which follows the longest deprivation period of 8-12 h without a food opportunity, and that the last opportunity is always the smallest meal. At low FUP, this can be understood as a satiety function – the mice have already eaten ~250 pellets – but at high FUP when overall intake is too low to sustain intake, the pattern persists. This is a facet of what we have termed above as “elective anorexia” but it could also be related to the fact that the last food opportunities were at the end of the night or early in the daytime. This suggests a possible interaction between food demand and either illumination *per se* or an endogenous circadian oscillator, and future studies are needed to test this hypothesis.

In the second experiment, we examined compensation within meals for between-meal snacking. Non-snacking mice eating at 8 opportunities per day performed comparably to the corresponding group in Experiment 1 in terms of change in food intake at FUP2 vs FUP25, and % of feeding opportunities taken. However, for reasons we do not understand, the first meal was smaller than in experiment 1. Mice with 3 snack opportunities ate ~25% of their energy from sucrose at FUP 2, and reduced their pellet intake by an identical amount. Similarly accurate compensation in maintenance chow intake by mice fed a “dessert” snack has been reported by Robertson and Rowland (2005) and in rats with a sugar solution (Lea and Roper 1977). At FUP25 when pellet intake was reduced by ~40% from FUP2, the intake from sugar rose to ~50% of the total intake and was also higher in absolute amount than during the FUP2 phase. As a result, energy intake of the snacking group exceeded that of non-snackers during FUP25, and they lost less body weight: that is, free snacks promoted total intake when food was costly. There was no gross difference in the temporal pattern of food consumption between snacking and non-snacking mice (Table 1), despite the fact that relatively large sugar snacks intervened in the middle part of the access period. That is, to the extent that caloric compensation occurred, it was spread over the entire feeding period and was not restricted to periods immediately after snacks. Thus, when the unit price of maintenance food is relatively high, mice took advantage of free sugar calories to a relatively greater extent, and used this to partially offset the decline in demand due to the higher unit price. The self-selected protein-to-calorie ratio during FUP25 for snackers was ~12% (half the manufacturer’s stated content of the pellet diet), and this may represent a limiting factor on higher consumption of the snack under these conditions.

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Highlights

- Mice with imposed meal frequencies showed unexpectedly elastic food demand functions
- Mice often did not feed maximally at every opportunity despite marked weight loss
- Free sugar snacks between meals reduced pellet intake in a cost-dependent manner

Figure 1.

Panel A shows mean food demand for the three feeding opportunity groups (4, 8, 16) as a function of the fixed unit price (FUP) for each 20-mg pellet. Data are group averages (N=5) averaged for the last 2 days at each FUP. Intake decreased significantly with unit price, but did not differ between the three groups. Panel B shows the corresponding body weights at the end of each experimental phase.

Figure 2.

Mean (+SEM) food intakes in the period of food availability, by quartile. For the 4 opportunity group, this is the four 40 minute meals. For the 8 and 16 opportunity groups, this corresponds to averages of 2 and 4 meals, respectively, but with total access time always 40 minutes. Intakes declined with increasing fixed unit price. Intakes also showed significant differences between the various meal clusters within a group and price condition (different superscripts indicate $p < 0.05$).

Figure 3.

Distribution of meal sizes in bins (0=0 to 9, 10=10 to 19, and so on) as a function of group and FUP phase of the experiment. Each datum is the average for 5 mice (4 at FUP25) and the last 2 days at each phase. For the zero size category most of the component data points were actually zero.

Figure 4. Mean numbers of pellets taken in successive 5 min periods of the 40 min meals in the 4 opportunity group. Each data point is the average of 5 mice on the last 2 days at each FUP; opportunities with zero intakes are included in these averages.

Figure 5.

Mean daily caloric intake of snacking and non-snacking groups of mice during the last 2 days of FUP2, FUP25, and return to FUP2 phases. Within each phase the left three bars show, respectively, the pellet, sugar, and total intakes of the snacking group, while the right hand bar shows the intake of the non-snackers (pellets only). *Intake differs significantly ($P < 0.05$) from each of the corresponding FUP2 phases. #Intake of non-snackers significantly lower than total intake of snacking group ($P < 0.05$).

TABLE 1

Mean number of pellets consumed in each successive feeding opportunity, the % of mice eating in that interval, and the intake from sugar snack in the intervals shown in snackers, and for non-snackers

	FUP2 Non-snackers	FUP2 Snackers	FUP25 Non-snackers	FUP25 Snackers	FUP2 Non-snackers	FUP2 Snackers
Meal 1	15.7 (37%)	15.2 (44%)	10.2 ^a (44%)	12.6 (31%)	16.6 ^a (31%)	12.2 (37%)
Meal 2	9.5 ^a (25%)	0.6 ^a (6%)	5.7 ^a (25%)	0 ^a (0%)	18.7 (44%)	0 ^a (0%)
Meal 3	30.7 (75%)	21.4 (75%)	20.0 (56%)	10.0 (37%)	30.9 (75%)	14.4 (81%)
Snack 1	---	0.9±.2 kcal	---	2.2±.2 kcal	---	1.3±.1 kcal
Meal 4	39.6 ^b (87%)	30.5 (93%)	21.9 (69%)	12.5 (62%)	48.7 ^b (94%)	37.5 ^b (100%)
Snack 2	---	1.5±.3 kcal	---	1.8±.3 kcal	---	1.7±.2 kcal
Meal 5	41.7 ^b (100%)	26.6 (87%)	34.6 ^b (100%)	13.6 (62%)	44.6 (100%)	26.9 (94%)
Snack 3	---	1.4±.3 kcal	---	2.2±.3 kcal	---	1.9±.3 kcal
Meal 6	41.4 ^b (93%)	45.6 ^b (93%)	31.2 (100%)	28.1 ^b (87%)	42.2 (87%)	39.6 ^b (94%)
Meal 7	33.7 ^b (93%)	25.0 (69%)	21.1 (87%)	23.1 (81%)	37.0 (87%)	29.0 (87%)
Meal 8	30.2 (81%)	17.7 (69%)	15.1 (44%)	10.5 (50%)	20.4 (62%)	15.6 (81%)

Note: Shown are means for 8 mice over 2 days at each FUP. The means include zero intake intervals. Intakes within a column bearing different superscripts are significantly different from each other (P<0.05)