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Activity-Based Anorexia in Rats as a Function of Opportunity to Run on an Activity Wheel

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This study concerns the effects of opportunity to run on activity-based anorexia in rats. Animals were allowed different amounts of time to run on wheels while exposed to a restricted feeding schedule of one 90-min meal per day. Generally, the incidence of strong anorexia increased when opportunity exceeded 12 h of access to a free wheel. Statistical analysis suggested that food intake declined with more opportunity and this decline was a function of the daily rate of change in wheel running. Body weight decline was due to the indirect effects of activity on food intake and the direct effects of rate of wheel running on energy expenditure.

Key words: rats, activity, anorexia

INTRODUCTION

When rats and mice are fed once per day (typically 1 h for rats and 3 for mice) they initially lose weight but over a few days adjust food intake and survive. However, animals exposed to the same food schedule but allowed free access to a running wheel *except while being fed* continue to lose body weight and die [Hall and Hanford, 1954; Spear and Hill, 1962; Rottenberg and Kuznesof, 1967; Rottenberg, 1968; Epling et al., 1981]. These animals also demonstrate an excessive increase in locomotor activity as measured by wheel revolutions turned per day [Epling et al., 1981]. The typical rat exposed to free wheel and restricted food demonstrates a moderate number of wheel turns for the first few days followed by a substantial increase which may go as high as 20,000 revolutions per 23-h period. Body weight for this animal shows a daily decline and if allowed to continue results in death. Finally, food intake initially goes up over days but as activity increases levels off and as activity peaks drops to

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low values. This process has been termed "self-starvation" by Routtenberg and Kuznesof [1967] and "activity-based anorexia" by Epling et al. [1983].

With one exception, studies of this phenomenon [Routtenberg and Kuznesof, 1967; Routtenberg, 1968; Epling et al., 1981] have allowed free access to an activity wheel except when animals were given their daily feeding period. The first of five studies reported by Routtenberg and Kuznesof [1967] allowed rats a 30-min per day feeding time and restricted access to the wheel for up to 2 h before and 2 h after being fed. Control rats on the same feeding schedule stabilized body weight but all experimental subjects continued to lose weight and died. Another experiment in this series of investigations restricted wheel access 3 h before a 60-min feeding period. This procedure did not significantly affect food ingestion and three of five rats self-starved. Importantly in these experiments, subjects were allowed a minimum of 20 h of free access to a running wheel. Thus, opportunity time for activity has not been systematically investigated.

Even for the free-feeding rat, forced or freely available activity results in a decrease in food intake. Premack and Premack [1963] demonstrated that introduction of an activity wheel produced running on the wheel and a subsequent decrease in food ingestion over the first 7 days of exposure. Levitsky [1974] has shown that rats on free food reduce the number of meals consumed per day when an activity wheel is introduced. Food intake was severely depressed, for the active animals, for the first 4–6 days after the wheel was presented to them. Stevenson et al. [1966] report that rats who were forced to run on a treadmill ingested less food than when they were not required to run.

Several studies have shown that short periods of high-intensity exercise decrease food ingestion in male rats [Oscai and Holloszy, 1969; Crews et al., 1969; Ahrens et al., 1972]. Katch et al. [1979] demonstrated that male rats given short-duration exercise of high intensity reduced food intake when compared to subjects which were exposed to long-duration exercise of low intensity. Both groups showed a reduction in caloric intake when compared to a control group. This finding is interesting since it implies that rate of activity may be an important variable in animal self-starvation. Finally, there is evidence that the *free-feeding* animal will eventually adjust food intake upward to compensate for increased activity [see Tokuyama et al., 1982; also, Mondon et al., 1980]. Apparently, the process of self-starvation requires both an activity source and the presence of dietary restriction.

Limiting opportunity to run in an activity wheel should have a direct effect on anorexia. Self-starvation would be less likely since net opportunity for running would be reduced. However, since a restricted food schedule generates increased locomotor activity the animals could compensate by increasing their rate of wheel running. Additionally, Epling et al. [1983] have suggested that *rate of change* in activity may be an important factor that generates the self-starvation effect. Restricting opportunity for activity would impose a ceiling on net amount of wheel running and thus limit the rate of change in daily activity.

At the present time there are no animal anorexia studies that systematically vary opportunity for activity in order to document its effects on food intake and body weight. Previous investigations have always provided 20 h or more of wheel access to a food-restricted animal. Given that excessive levels of activity are important to self-starvation, then reduction of opportunity should be a major variable affecting this process. Thus, this study is designed to vary time of access to an activity wheel and explore its effects on self-starvation in rats.

METHOD

Subjects

Forty-two albino male Sprague-Dawley rats were 38 to 42 days old when obtained from the University of Alberta animal colony. Seven subjects at a time were selected from batches of 14 nonlittermates on the basis of an activity test (see Procedure section). This selection attempted to reduce variability in initial activity levels within and between experimental conditions prior to treatment. All subjects were individually housed and randomly assigned to conditions and wheels at 43 to 47 days old.

Apparatus

Seven standard Wahman running wheels (35 cm in diameter) equipped with side cages (14.5 cm × 24 cm) served as the living environment during the experiment. A sliding door separated cage and wheel during feeding periods. Each wheel was modified with a braking device that was mounted on the side plate above the wheel. The brake was a metal shaft with a notched-rubber tip that could be raised or lowered on the basis of Coulbourne solid-state programming equipment. Wheels were also equipped with a mechanical counter and a microswitch, both of which were incremented by a revolution in either direction. A Coulbourne Instruments printout counter and two Gerbrands cumulative recorders provided data on wheel turns. All control equipment was situated in a separate room. A Sartorius electronic scale was situated in the experimental laboratory and provided measures of body weight, food and water intake.

Procedures

A "run test" was administered to each animal on the day of arrival at the laboratory. This was a 2-h activity assessment that measured each animal's initial level of wheel running. The test was conducted in a separate room on Wahman activity wheels. The number of revolutions in 2 h, during which the rats were restricted to the wheel, was the test measure. Next, the seven most active animals were selcted as subjects and placed on free food in their home cages. A 5-day baseline was used to measure body weight and food intake. During this period and subsequent experimental days, animals were on 24-h continuous light, and food was Wayne Lab-Blox, a standard commercially available laboratory chow. Preexperimental measures were taken between 11:00 A.M. and 1:00 P.M. of each day.

When the baseline was completed, animals were randomly assigned to experimental conditions and running wheels. During the experimental phase, animals lived in their wheels with attached side cage. Water bottles were continuously available, but food was restricted to a single 90-min feeding period per day. Food was preweighed and the day's food supply only allowed to vary between 25 to 30 gms. This quantity of food typically exceeded the amount ingested by most animals during the free-food baseline and was always more than that consumed on the restricted-food schedule.

The experimental phase began with animals being transferred from their home cages to the running wheel side cage at 11:00 A.M. on the fifth day of baseline. The doors to the wheels were closed until 1:00 P.M., when the brakes were released and the animals had the opporutnity to enter the wheel and run until programmed timers activated the brakes. On subsequent days, animals were placed in the side cage with the door between the wheel and cage closed for this same 2-h period. During this time, the rats were fed for 90 min, and all dependent measures were obtained. Six experimental conditions varied opportunity to engage in wheel running by scheduling the amount of time that wheels were operative (i.e., time of brake-off). A control group was exposed to the same procedure, but wheels were always braked for these animals. Experimental groups consisted of 2, 6, 12, 18, and 22 h of free wheel. Free wheel was timed from the end of the side cage restricted period (i.e., at 1:00 P.M. each day).

Dependent measures were daily wheel turns, body weight, and food intake. Body weight in grams and number of wheel revolutions were recorded after the animals were moved to the side cage and before the feeding period. Food intake in grams was based on the differences between pre and post measures (spillage was not separated from the post measure since it was generally slight and mixed with urine and feces). Animals were removed from the experiment at 70% of their free-feeding body weight or when weight on day 4, or any 4-day period, was equal to or greater than weight on day 1. The criterion for removal was necessary for ethical reasons and the weight stability criterion is in accord with previous research [Routtenberg and Kuznesof, 1967; Routtenberg, 1968].

RESULTS

Preexperimental Measures

Initial analyses were conducted on the preexperimental measures. Table 1 portrays the means by condition for number of wheel revolutions in the run test (prerun), body weight based on the fifth day of baseline, and food intake averaged over the 5-day preexperimental period. Separate one-way analyses of variance indicated no significant differences on any of these measures. These results suggest that the treatment groups were equated on these factors prior to the experimental phases.

Data Preparation

Since opportunity for activity may differentially affect running, eating, and body weight over experimental days, it is necessary to provide a trend analysis as part of the design. However, animals attained 70% removal or weight stability criteria in different amounts of time (i.e., days in the experiment). In order to standardize the results with respect to time in the experiment, both linear and nonlinear regression techniques were used to fit individual functions for the three dependent measures. For each subject, the dependent variables were regressed on days in the experiment, and best-fit curves were used to interpolate four values for each dependent measure. Since 4 days was the shortest time to criterion for any subject, data are reported over four quarters of the total experimental time.[1] Based on this interpolation procedure, a 6 ×

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[1] Previous reports by Epling et al. [1981a,b, 1983] have employed an interpolation procedure suggested by Vincent [1912]. This procedure, however, is less adequate when observations depart from linearity. Inspection of the individual data suggests that the dependent measures may be nonlinear in cases of strong anorexia (i.e., activity appears in exponential form). Regression analysis fits individual curves with the median r^2 equal to .95 for body weight, .89 for wheel-revolution, and .79 for food intake. The lower explained variance for food intake is due to the variability introduced through spillage which could not be accurately assessed in this study. However, the overall fit by regression analysis is more than adequate for the food intake measure.

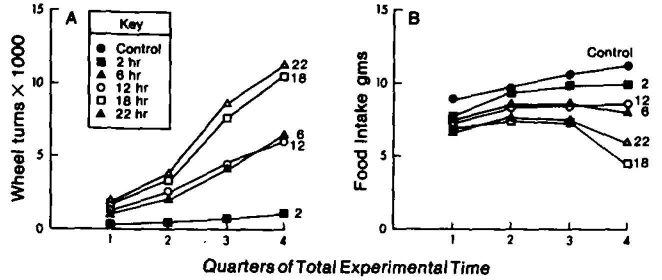

Fig. 1. The effect of opportunity to run on amount of wheel running (A) and level of food intake (B) shown over quarters of total time in experimental (see Data Preparation section).

TABLE 1. Mean and Standard Deviations Preexperimental Values for Run Test Measured in Number of Wheel Turns and Body Weight and Food Intake in Grams by Treatment Condition*

	Condition (h access)					
Measure	22	18	12	6	2	Control
Prerun	343.9 (172.6)	382.1 (190.7)	334.1 (217.8)	351.0 (280.4)	295.1 (197.4)	311.6 (115.4)
Preweight	212.7 (35.3)	208.7 (42.6)	204.4 (39.9)	205.6 (26.2)	206.8 (30.9)	204.5 (34.2)
Prefood	22.9 (3.7)	20.9 (4.1)	18.6 (3.7)	19.9 (1.8)	19.9 (3.1)	20.5 (3.2)

*Standard deviations in parentheses.

4 repeated measures analysis of variance was the basic design. There were six levels of opportunity (i.e., control, 2, 6, 12, 18, and 22 h) as the between-groups factor and four levels of experimental period (i.e., first, second, third, and fourth quarters of the experiment) as the within-groups variate.

Analysis of Wheel Running

An initial question is whether opportunity for activity affects (a) overall amount of wheel running and (b) the rate of change in wheel running over the four experimental quarters. Analysis of variance (excluding the no-activity control group) indicates that opportunity has a main effect on the number of wheel revolutions, $F(4,30) = 10.06$, $P < .001$. The mean number of wheel revolutions is ordered by amount of opportunity: 22 h ($M = 6,368.5$), 18 h ($M = 5,820.3$), 12 h ($M = 3,558.2$), 6 h ($M = 3,538.9$), and 2 h ($M = 649.2$). There is also an effect of experimental quarter, indicating an increase in wheel running by time in the experiment, $F(3,90) = 47.25$, $P < .001$.

Most importantly, there is a significant interaction of opportunity by quarters of the experiment, $F(12,90) = 3.57$, $P < .001$. This interaction is portrayed in Figure 1A.

A trend analysis [Winer, 1971] decomposes the interaction sums of squares into linear, quadratic, and cubic components. There is a significant difference in linear trend by condition, $F(4,30) = 6.89$, $P < .001$, but higher-order components are not significant. The significant linear trend (i.e., slope) can be interpreted as differences in the rate of change in activity over experimental quarters. Figure 1A indicates that the highest rate of change in daily wheel running occurs in the 22-h and 18-h conditions, where opportunity is greatest, and the least amount of change occurs in the 2-h group, where opportunity is most restricted. The daily change in wheel running for the 12-h and 6-h conditions is remarkably similar. Either the extra amount of time for the 12-h animals does not enhance wheel running relative to the 6-h subjects, or the wheel restriction of the 6-h group produces more running per opportunity than the 12-h condition.

The latter hypothesis is tentatively supported; analysis of variance on the amount of wheel running per opportunity indicated a weak interaction of condition with experimental quarter, F(12,90) = 1.62, $P < .10$.[2] Further analysis indicated a difference in linear trend, F(4,30) = 2.11, $P < .10$. Examination of the mean rate by experimental quarter indicated that the 6-h condition had a more accelerated slope than other conditions. This group had the highest rates over all experimental quarters. While the main effect is not significant, F(4,30) = 2.04, P = .114, owing to substantial within-group variance, it is interesting to examine the mean values by condition. The 6-h group (m = 589.6) showed roughly twice the amount of wheel running per opportunity hour when compared to the 12-h group (m = 296.3), and this difference holds for the 22-h (m = 289.2), 18-h (m = 323.1), and 2-h (m = 324.6) conditions. Apparently, there is a "compensation effect" operating to counterbalance restricted opportunity in this group. Animals in the 6-h condition substantially increase activity during their period of allotted time.

Food Intake

Previous results showed that the number of hours of access to a running wheel ordered rate of change in activity. Since it is hypothesized that food intake is influenced by rate of change in activity, food ingestion should be a function of opportunity for free wheel. Specifically, conditions with little or moderate opportunity for wheel running would be expected to show suppression of eating relative to the control group given the same 90-min food restriction. As opportunity increases, and rate of change in activity accelerates, food intake should decline (i.e., activity anorexia occurs). Analysis of variance indicates a significant main effect of opportunity to run on food intake, F(5,36) = 3.38, $P < .02$. The means are 7.1, 6.5, 8.3, 8.3, 9.3, and 10.2 gms of food respectively for the 22, 18, 12, 6, and 2-h, and control conditions. There is also an effect of experimental quarter, F(3,108) = 8.64, $P < .001$.

More importantly, the interaction of opportunity and experimental quarter is significant, F(15,108) = 3.49, $P < .001$. Figure 1B portrays this interaction effect and trend analysis decomposes the variance into linear and higher-order components. There is a significant difference in linear trend by condition, F(5,36) = 3.63, $P < .008$. Notably, the control and 2-h conditions have positive trends for food intake, indicating an increase in consumption over experimental quarters. The animals in the

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[2] The hypothesis that the 6-h condition produces more running per opportunity period is exploratory. Previous unpublished results by Knoll-MacKenzie [1983] reported a significant difference in rate of wheel running for this condition. While the present results are not significant at the .05 level, they are consistent with Knoll-MacKenzie's findings. The higher alpha level is more likely due to greater within-group variability than to the truth of the null hypothesis. Also, the assumption that rate varies by condition ordered other findings in this report.

12- and 6-h conditions show no tendency to increase intake, and these subjects suppress consumption relative to the control condition. The animals in the 18- and 22-h groups demonstrate a downward trend (i.e., negative) over experimental quarters, indicating a reduction of eating. Both of these groups appear to sharply drop intake from quarter 3 to quarter 4. This results in curvature in the trend lines and appears in the analysis as a significant quadratic effect, F(5,36) = 2.70, P < .04.

The 18-h condition shows the greatest decline in food intake, rather than the 22-h group. This may be due to one animal in the 22-h condition that improved intake over days while all others declined. This weakened the results relative to the 18-h condition where all animals showed a suppression or reduction of intake. Notably, the 22-h animal that improved food intake also failed to show high amounts of activity.

In order to test the assumption that suppression and reduction of food intake by opportunity was due to variation in wheel running,. an analysis of covariance suggested by Winer [1971, p. 806] was conducted. In this design, opportunity to run was the between-groups factor, experimental quarter was the within-groups variate, and level of wheel running was a covariate that changed over experimental quarters. If difference in food intake by opportunity was due to wheel running, then the previous effects of conditions would no longer be significant and the covariate, level of wheel running, would explain the variation in food intake. In accord with this expectation, the covariate is significant, F(1,35) = 12.76, P < .001, and neither the condition main effect, F(5,35) = 0.33, n.s., nor the interaction of condition with the experimental quarter, F(15,107) = 1.46, n.s., is now significant. This is strong evidence that opportunity for activity produced differences in food intake by altering the level of wheel running of animals on food restriction. Comparing Figure 1A and 1B, it is clear that change in level of running accounts for the degree of food reduction over experimental quarters.

Body Weight

If body weight reflects the effects of total amount of activity on food intake, the 18-h and 22-h conditions should demonstrate the greatest decline in weight followed by the 6- and 12-h treatments.[3] Finally, the 2-h group should show greater weight decline than the control (no opportunity) condition. While there is no main effect, analysis of variance reveals a significant interaction of the conditions by quarters of the experiment, F(15,108) = 3.66, P < .001. This interaction is portrayed in Figure 2 (unadjusted).

There is a significant difference by condition in linear, F(5,36) = 3.77, P < .008 and quadratic, F(5,36) = 3.62, P < .009, trends. The quadratic component can be assigned mostly to the control group that loses and then begins to recover body weight. The most interesting aspect of the linear trend is the steep decline in weight for the 6-h condition. This weight reduction is more than expected on the basis of food intake and activity-level data. However, recall that this condition generated an increase in *rate of wheel running* that exceeded the other experimental conditions (see footnote 2). In order to assess whether this increase in rate accounts for the strong decline in weight in the 6-h group, an analysis of covariance was conducted. In this

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[3] While the wheel running results suggest that the 22-h group will show the largest decline in body weight, recall that one animal in this condition did not run at high levels and increased food intake.

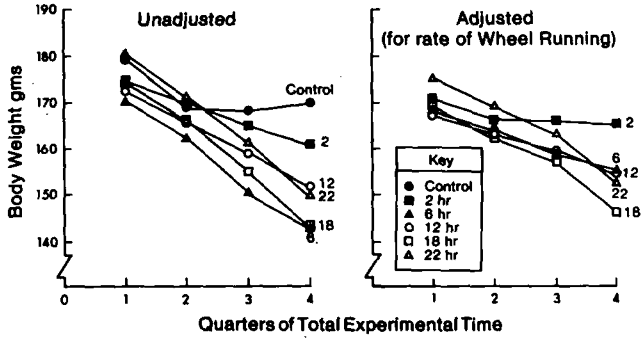

Fig. 2. The effects of opportunity to run on body weight shown over quarters of total time in experiment (unadjusted) and adjusted for the rate of wheel running (adjusted).

analysis rate of wheel running was treated as a covariate that changes over the experimental quarters [Winer, 1971, p. 806]. Opportunity to run and quarters of the experiment were between and within factors, respectively. The analysis was conducted omitting the control group since rate could not vary for this condition. Figure 2 (Adjusted) displays the mean weights when adjusted for the effects of the rate covariate. The opportunity to run with experimental quarter is still significant, $F(12,89) = 2.46$, $P < .009$, but the nature of the interaction has changed with the effects of the rate covariate, statistically controlled, $F(1,89) = 31.37$, $P < .001$. Importantly, the 6-h condition now demonstrates a less severe decline in body weight, and the conditions are also well ordered in terms of food intake. Overall, these findings suggest that high-rate locomotor activity contributes to weight decline. This direct effect of rate or intensity of exercise on body weight is apparently over and above the indirect effect produced by level of activity on food ingestion.

Incidence of Anorexia

While the previous results strongly support the influence of opportunity to run on activity, food intake, and body weight, these separate analyses are not a direct assessment of anorexia. Previous investigators [Routtenberg, 1968; Routtenberg and Kuzenof, 1967] have defined anorexia in terms of ingestion of less than 1 gm of food during the meal period. Typically, an animal who has reached this criterion is only hours from death and there is little doubt of anorexia. Based on this criterion, rats may be classified as to self-starvation or survival. However, current ethical standards will not permit such a rigorous definition and the present research was guided by a 70% body-weight criterion.

In order to classify animals in terms of anorexia, the individual functions used for interpolation were examined. It was possible to define four "effects" on the basis of the regression curves for food intake and body weight on days in the experiment. Figure 3 presents idealized curves that were used to classify the individual functions as the "effect" type.

These idealized curves are portrayed on the same coordinates with the scales adjusted for each measure. The "strong anorexia" effect is presented in Figure 3A. Here body weight is declining, with some downward acceleration occurring during the last few days. Food intake is low upon entry into the experimental phase but tends

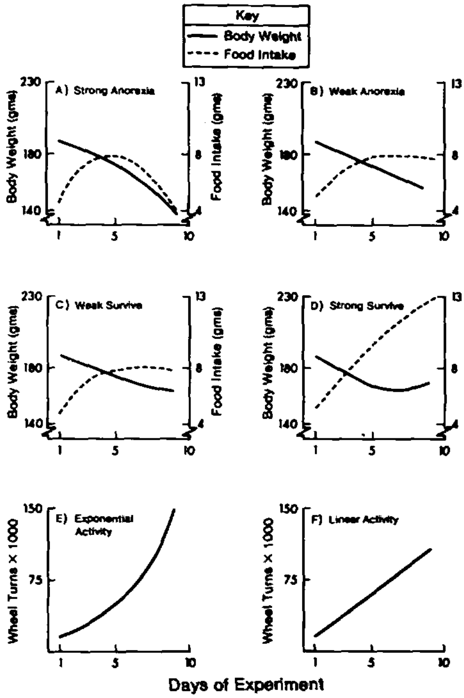

Fig. 3. Idealized functions for body weight and food intake that allowed for classification of four effect types. Also, wheel running curves associated with strong anorexia (exponential) and survival or weak anorexia (linear).

to increase over the first few days. This is followed by a leveling off of intake and then a final period of decline. Since body weight is declining, and food intake leveling and then dropping, there is clear evidence that the animal is no longer defending body weight, and hence "strong anorexia" is defined. Some subjects, however, did not show the reversal in food intake by the time of 70% body-weight criterion. While body-weight curves were trending downward (see Figure 3B), the food intake for these subjects rises and then levels off. Typically, this "leveling off" in consumption is well below the food ingestion of control animals, and intake may be termed *suppressed* for these subjects. Since body weight is on a downward trend and food intake is still not sufficient to maintain weight, these subjects are classified as "weak anorexias."

In addition to these anorectic effects, if is possible to define two survival patterns. Figure 3C depicts a "weak survival" effect, where body weight declines and then levels off and food intake initially increases but also levels. Intake is sufficient to prevent body weight decline but not sufficient to push body weight toward baseline levels. Figure 3D represents a "strong survival" effect, which typically shows body weight falling, leveling, and then tending to increase (i.e., recovery). Food consumption shows a linear increase over days with this rise being limited only by the single meal presentation.

This classification scheme was employed to categorize type of effect for each of the 42 rats. Reliability of classification was assessed by having one researcher code the curves in a randomized sequence and the other researcher code the same curves in a different order. All coding was done blind to condition and previous judgment by the other experimenter. There was 95% agreement using this classification system. In the two cases of nonagreement, a strong versus weak anorectic effect was in dispute. In both cases, the dispute was settled by assigning the case to the weak effect. It is important to note that a survival effect was never classified as an anorectic effect or vice versa. Also, while the weak survival effect was empirically observed, only one animal in the control condition demonstrated this pattern. When animals survived, the strong survival pattern was most prominent.

In order to conduct a chi-square test for association, the data were collapsed into survival and anorectic effects and the frequencies distributed by experimental condition. The association between experimental condition and effect type is significant, $F = 20.19$, $df = 5$, $P < .002$, but some caution must be taken, since expected cell frequencies were less than five. Table 2 presents the results of this analysis. Compared with the control group (no opportunity to run), which shows no cases of anorexia, even 2 h of opportunity for activity substantially increases incidence (i.e., 42.9% anorexia). Also, while the percentage of anorexia is generally associated with greater opportunity, the 6-h condition is again unusual in terms of the high percentage (85.7%) of anorexias. A more detailed examination of the type of anorexia (strong versus weak) indicated only a single case of strong anorexia in each condition of 12 h or less opportunity. Thus, most anorexias in the 6-h condition were "weak" according to the classification procedure. On the other hand, all seven cases of anorexia in the 18-h condition and four of the six cases in the 22-h condition were of the "strong" type. This suggests that incidence of strong anorexia is associated with opportunity for activity exceeding 12 h of access to a running wheel.

It is important to examine the activity curves (from regression analysis) of animals classified as strong or weak anorectics. Figure 3E,F portrays two activity patterns as idealized curves. The exponential increase in activity over days *always* occurred with animals classified as strong anorectics. In some subjects the accelerated running would drop off (but still remain quite excessive) a day or two before removal from the experiment [see Routtenberg, 1968]. At this time, food intake was low and, presumably owing to starvation, the animal was having difficulty maintaining running. This activity pattern was not found in weak anorexias, but rather these anorexias were characterized by a medium to high linear increase in running over days (see Fig. 3F). All animals demonstrating the survival pattern showed either no daily increase or low linear increases in activity. Thus, it appears that strong anorectic animals were self-starving because of the accelerated activity pattern that this pattern becomes more frequent with opportunity to run.

DISCUSSION

The present study focused on the effects of opportunity for wheel running on activity-based anorexia. Results indicate that the incidence of such anorexias increased as rats were allowed more time per day on the wheel. Further, the occurrence of strong anorexias, where an animal reduces food intake in the presence of declining body weight, is also a function of time and access to an activity source.

Examination of the individual data indicated that anorexias occurrred when activity showed an accelerated function over days. When activity was at low levels,

TABLE 2. Incidence, in Percentage, of Anorexia and Survival Effects by Experimental Condition (Frequency in Brackets)

	Condition (h access)					
Effect type	22	18	12	6	2	Control
Anorexia	85.7 (6)	100.0 (7)	57.1 (4)	85.7 (6)	42.9 (3)	00.0 (0)
Survival	14.3 (1)	00.0 (0)	42.9 (3)	14.3 (1)	57.1 (4)	100.0 (7)
Total cases	7	7	7	7	7	7

or a linear function was generated, strong anorexia did not occur. Animals showing these patterns survive or show weak anorexia, respectively. Independent of the opportunity condition, if an animal did not run at increasingly excessive levels then the subject always survived. As running reduces to lower and lower levels the incidence of strong survival, where an animal defends body weight by increasing food intake, substantially increases [Mrosovsky and Sherry, 1980]. However, opportunity for low levels of activity affects chances of meeting survival criterion. This is illustrated by comparing the incidence of survival in the control versus 2-h condition. Even 2 h of wheel access reduces survival effects from 100% to 57%.

Statistical analysis of wheel running demonstrated that, in general, the overall amount of running was ordered by time of access to the wheel. As number of hours access increased the mean number of revolutions per day also increased. The exception was the 6-h condition, which showed as much total activity as the 12-h group. The mean change in daily activity, again with the exception of the 6-h condition, was also a function of access time. Evidence indicated that the unusual level of activity displayed by 6-h animals was due to an increased rate of wheel turns per opportunity hour. Thus, these rats ran faster than other groups during their allotted time period. When compared with 12-h subjects, these animals show a “compensation effect” where they make up for restricted opportunity by increasing rate of running. This same compensation phenomenon by 6-h animals has been reported in an unpublished masters thesis by Knoll-MacKenzie [1983]. Determining the exact basis of this effect requires further research.

In this study, body weight appears to be a function of food intake, which is in turn a function of rate of change in daily activity. The exception to this statement occurs in the 6-h opportunity group. This group demonstrated a greater reduction in body weight than expected on the basis of the food intake results. Based on the covariance analysis, it appears that the 6-h anomaly is due to the high rate of running produced by this condition. Thus, body weight can be affected by strenuousness of exercise, independent of the indirect effects of exercise on food intake. Essentially, some reduction in weight occurs as a function of caloric expenditure. However, most of the anorectic effect was due to the debilitating effects of locomotor activity on food consumption.

Both the 18- and 22-h access conditions operate to reduce mean food consumption over days. The other conditions produce suppression of food intake relative to the locked-wheel control group. Results of analysis of covariance suggested that the rate of change in daily wheel running accounted for the variance in food consumption by condition. Time of access to the wheel limited the rate of change in daily activity and food intake was a function of this change. Thus, as opportunity allows for increasing amounts of activity, food intake is correspondingly suppressed and/or reduced.

Generally, the current findings suggest that *rate of change* in daily amount of activity is critical to the development of strong anorexia in rats. Such results are in accord with several studies that have demonstrated that high-intensity exercise produces decreased food consumption in rats [Oscai and Holloszy, 1969; Crews et al., 1969; Ahrens et al., 1972]. Katch et al. [1979] demonstrated that male rats, exposed to high-intensity exercise, showed a decrease in food consumption when they were compared to a low-intensity exercise group that was matched for caloric expenditure. Both exercise groups ingested less food than no exercise controls. In the present study, intensity of exercise changed on a daily basis, and this change in intensity was directly related to food intake levels. Apparently, the greater the change in intensity of exercise, the less food consumed. Taken together, these results argue that high-intensity locomotor activity operates on the mechanisms which control feeding [see Kanarek and Collier, 1983]. The present study extends this observation and suggests that controlling opportunity for an activity source affects intensity of exercise, and thus orders food consumption.

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