*DEPRIVATION AND SATIATION: THE INTERRELATIONS
BETWEEN FOOD AND WHEEL RUNNING*

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Two experiments were designed to assess whether depriving rats of food would increase the reinforcement effectiveness of wheel running (Experiment 1) and whether satiation for wheel running would decrease the reinforcement effectiveness of food (Experiment 2). In Experiment 1, a progressive-ratio schedule was used to measure the reinforcement effectiveness of wheel running when rats were deprived or not deprived of food. Completion of a fixed number of lever presses released a brake on a running wheel for 60 s, and the response requirement was systematically increased until the rat stopped pressing or until 8 hr had elapsed. The ratio value reached (and the total number of lever presses) was an inverted-U function of food deprivation (percentage body weight). In Experiment 2, when wheel running preceded test sessions, fewer food-reinforced lever presses were maintained by the progressive-ratio schedule, and responding occurred at a lower rate on a variable-interval schedule. An interpretation of these results is that deprivation or satiation with respect to one event (such as food) alters the reinforcement effectiveness of a different event (such as access to wheel running).

Key words: wheel running, eating, establishing operations, reinforcement effectiveness, lever press, rats

Depriving an organism of some event is the most common procedure to increase the reinforcing effectiveness of that event. Conversely, giving the organism access to an event usually decreases the reinforcing effectiveness of the event (satiation). Such procedures alter "the effectiveness of some object or event as reinforcement and simultaneously . . . [alter] the momentary frequency of the behavior that has been followed by that reinforcement" (Michael, 1982, pp. 150-151) and are termed establishing operations (Keller & Schoenfeld, 1950; Michael, 1982). Although the effects of deprivation and satiation are sometimes considered to be specific to the event whose access has been altered, the effects are not always specific. For example, depriving a rat of lab chow alters the reinforcing effectiveness of sucrose. That is, lab-chow deprivation can be

described as an establishing operation for sucrose. Such cross-event effects also have been described in terms of the economic concepts of *substitution* and *partial substitution* (Hursh, 1980; Lea, 1978; Rachlin & Krasnoff, 1983). However described, it is especially interesting when deprivation or satiation with respect to one kind of event alters the reinforcing effectiveness of events that we intuitively consider unrelated. Some examples follow.

Light onset can function as primary reinforcement for bar pressing in rats (Girdner, 1953; Kish, 1955, 1966; Marx, Henderson, & Roberts, 1955). Further, the reinforcing effectiveness of light onset increases as a function of food deprivation (Davis, 1958; Forgays & Levin, 1958; Roberts, Marx, & Collier, 1958; Segal, 1959) and of water deprivation (Clayton, 1958).

Our research on activity-based anorexia in rodents (Epling & Pierce, 1984; Epling, Pierce, & Stefan, 1981, 1983) and other research on self-starvation (Kanarek & Collier, 1983; Routtenberg, 1968; Routtenberg & Kuznesof, 1967) suggests that the reinforcing effectiveness of food and wheel running may interrelate. For example, wheel running in rats increases when eating is restricted to a single daily meal (Epling et al., 1983). Such meal restriction typically results in decreased food consumption, accompanied by a decline in

This research was funded by Grant 55-66016 from the Alberta Mental Health Research Council and by a Natural Science and Engineering Research Scholarship awarded to Douglas Boer. We would like to express our appreciation to Karen Pawluski, who corrected our grammar and spelling and who typed the draft and final copies. Thanks are also due to the technical staff of our psychology department for motorizing the running wheel for use in Experiment 2. Reprint requests may be sent to W. David Pierce, Department of Sociology, The University of Alberta, Edmonton, Alberta T6G 2H4, Canada or to W. Frank Epling, Department of Psychology, The University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

Fig. 1. Modified Wahmann running wheel used to study lever pressing reinforced by 60-s access to wheel running, as a function of percentage body weight. Portrayed is the retractable lever that was mounted on a metal plate that fit over the entrance to the wheel. Also shown is the brake that was controlled by a 24-V continuous-operate solenoid.

body weight. Yet as body weight decreases, the animal becomes increasingly active on the wheel; that activity, surprisingly, produces a further decline in food intake.

Many previous studies (Cornish & Mrosovsky, 1965; Duda & Bolles, 1963; Finger, 1951; Hall & Hanford, 1954; Reid & Finger, 1955) showed that depriving an organism of food resulted in a higher probability of wheel running. Such effects were sometimes interpreted as showing that food deprivation increases "general drive" as indexed by spontaneous activity (e.g., Teghtsoonian & Campbell, 1960).

Other studies demonstrated that physical activity reduces daily food intake (Ahrens, Bishop, & Berdanier, 1972; Crews, Fuge, Oscai, Holloszy, & Shank, 1969; Katch, Martin, & Martin, 1979; Oscai & Holloszy, 1969). For example, rats ate less per day when a running wheel was present than when it was absent (Levitsky, 1974; Premack & Premack, 1963). Further, rats ate less food when they were forced to run on a treadmill than when they were not required to run (Stevenson, Box, Feleki, & Beaton, 1966). The experiments re-

ported here were a further exploration of such relationships.

EXPERIMENT 1

The question addressed by Experiment 1 was whether food deprivation would increase the effectiveness of wheel running as reinforcement for lever pressing. Reinforcing effectiveness was assessed by a progressive ratio (to be described below). The question addressed by Experiment 2 was whether satiation of wheel running would decrease the effectiveness of food pellets as reinforcers for lever pressing. Reinforcement effectiveness was assessed by a progressive-ratio procedure (e.g., Hodos, 1961) and by the response rate sustained by a variable-interval (VI) schedule (e.g., Clark, 1958).

On a progressive-ratio schedule, reinforcement is dependent upon number of repeated responses, but that number changes systematically. At the beginning of the session, the number is small, but it becomes larger as successive reinforcers are obtained. The measure of interest is the highest response requirement the animal will complete before "quitting." Other things equal, the higher the ratio before quitting, the more potent the reinforcer is assumed to be (Hodos, 1961; Smith, 1974).

METHOD

Subjects

Subjects were 5 female and 4 male Sprague-Dawley rats, obtained from the University's animal colony. Animals were 50 days old at the start of the experiment and were kept under continuous light conditions in a room with a temperature of 20 ± 2 degrees Celsius. Food and water were freely available in the home cages.

Apparatus

A running wheel (Wahmann Co.) was equipped with a solenoid-operated brake. When the solenoid was activated, a rubber-tipped metal shaft contacted the wheel, causing the wheel to stop gradually. A retractable bar (Lehigh Valley Electronics) was mounted on a metal plate that fit over the entrance to the wheel (see Figure 1). Programming and recording equipment (Coulbourn Instruments) was located in a separate room.

Procedure

The initial procedure was designed to establish control of running by a 60-Hz tone. All animals were exposed to alternating periods consisting of the wheel being unlocked (accompanied by a 60-Hz tone) and the wheel being locked (accompanied by no tone). This procedure continued until running reliably occurred in the presence of the tone. Following this training, the retractable lever was extended into the wheel drum and a single lever press was required to retract the lever, turn on the tone, and free the wheel for 60 s. Subsequently, the number of presses required to free the wheel was gradually increased to 20 (fixed ratio 20), and each rat was given a single 1-hr session at this value. Subjects 1, 5, 7, and 8 were then reduced, over 16 days, to 75% of their free-feeding weights by limiting food to 10 g per day. Subjects 2, 3, 4, 6, and 9 were maintained at their ad-libitum weights (100% body weight). All animals (100% and 75%) were housed in their home cages during this 16-day interval. Because the test procedure could take up to 8 hr (see below), entry into the study was staggered. Thus, subjects were tested in the wheel apparatus on different days but total time in the experiment and age of subject were held constant.

Following the 16-day period, each animal was given a single test session, beginning at 8:00 a.m., consisting of a progressively increasing fixed-ratio schedule that gave access to the freely turning wheel and the tone for 60-s periods. At the start of the test session, five lever presses were required. After three completions at this value, the schedule requirement was increased to 10. After three completions with the ratio requirement of 10, the requirement was again increased by five to 15, and so on. The test session was continued until 1 hr had elapsed without the subject completing the ratio requirement or until the session length exceeded 8 hr.

Next, the subjects that had been tested under free food were reduced over 16 days to 75% body weight, and the subjects that had been deprived were placed on 16 days of free food. Subsequently, the animals were again tested with the progressive-ratio procedure at their new levels of deprivation. Thus, the design was counterbalanced for level of deprivation. The dependent variables were highest ratio completed during the test procedure and

Table 1

Total number of hours spent in the progressive-ratio test session as a function of percentage body weight. For order of exposure to level of deprivation, see Figures 2 and 3.

Subject	Percentage body weight				
	100	85	75	70	65
1	3.0 (3.8)		7.6		
2	6.1		8.0 (8.0)		
3	8.0	8.0	8.0	8.0	
4	8.0	8.0	8.0	8.0	
5	4.9	5.5	8.0	8.0	6.4
6	5.5		8.0		
7	3.3		5.4		
8	2.9		5.6		
9	2.5		6.2		

Note: Subjects 1 and 2 were exposed to an A-B-A design and the values in parentheses represent the return to baseline.

total number of lever presses emitted. For male subjects, data were obtained at 100% and 75% body weight; for female animals, data were obtained at additional values of percentage body weight. This was done because the females' behavior seemed more sensitive to the deprivation variable (see Figure 2).

To further assess the reliability of the results, Subject 1 was tested at 75% then 100% and again at 75% body weight, and Subject 2 was tested at 100%, 75%, and 100% levels. In addition, after Subjects 3, 4, and 5 were tested at the 100% and 75% levels of body weight, they were tested at other values of deprivation in order to more fully explore the relationship between food deprivation and reinforcement effectiveness of access to the wheel. Subject 3 was tested at the additional values of 70% then 85%; Subject 4 at 85% then 70%; and Subject 5 at 70%, 85%, and then 65%. For each value of deprivation, animals were brought to the specified weight by adjusting daily food allocation over a 16-day period (see above).

RESULTS

The effectiveness of wheel running as reinforcement was expected to be greatest under conditions of food deprivation. Table 1 presents the total number of hours that the rats spent in the progressive-ratio test session. Whenever an animal spent less than 8 hr, it met the 1-hr criterion (see above). Seven of the 9 rats spent less time in the test session at 100% body weight than at 75% body weight.

Table 2

Mean number of wheel revolutions per 60-s opportunity as a function of percentage body weight of female and male rats.

% body weight	Females					Males			
	1	2	3	4	5	6	7	8	9
100	21.7	15.8	38.2	30.1	17.4	17.9	8.8	8.5	9.5
75	28.1	32.4	36.6	32.2	25.7	17.7	21.3	17.8	15.8

Rats 3 and 4 met the 8-hr criterion at both levels of deprivation.

Figure 2 shows that the FR size sustained by access to the free-turning wheel was greater for all subjects under the 75% body weight condition than under the 100% condition. In general, differences in the maximum FR size were greater for the females than for the males (see especially the results for female Subject 2).

Table 2 presents the mean number of wheel revolutions per 60-s opportunity as a function of percentage body weight. The point was to see how "consumption" of the reinforcer varied with deprivation level. To rule out possible differences due to sampling from different ratio sizes, the means in Table 2 were calculated from data summed over equivalent ratio values for each animal. Thus, animals sustained higher ratios when they were food deprived; data from the latter part of the deprivation session were excluded. For 7 of the 9 rats, the mean number of revolutions per 60-s opportunity was higher at 75% than at 100% body weight. Thus, there is some correspondence between the effect of deprivation on running and on the maximum ratio of lever presses per reinforcement maintained by access to the wheel. However, the correspondence is not perfect, as indicated by the results of Rats 3 and 6.

Figure 3 provides further evidence on the reliability of the effect of food deprivation on the persistence of ratio responding reinforced by access to the free-turning wheel. Reinstatement of the original deprivation level (for Subjects 1 and 2) was accompanied by a corresponding change in the maximum ratio in the direction of the original performance at that deprivation level. There may have been, however, an order effect for both animals, inasmuch as the maximum ratio value was somewhat higher on the second exposure to a deprivation level than on the first exposure.

Figure 4 shows the results from Subjects 3,

4, and 5, which were exposed to additional deprivation levels. The total number of lever presses per session increased as a function of deprivation to a maximum of between 70% to 75% body weight. At the highest levels of deprivation, however, the number of lever presses emitted per session declined. Thus, it appears that the function may be described as an inverted U. The ordering of total lever presses per session corresponded closely with the ordering of the maximum size of ratio completed (see Table 3).

DISCUSSION

These results demonstrated that an establishing operation performed with respect to food (i.e., food deprivation) affected the rats'

Fig. 2. Maximum size of ratio completed on a progressive-ratio schedule, as a function of percentage body weight. Subjects 1 through 5 are females and 6 through 9 are males. The key shows order of exposure (i.e., 75% weight then 100%) with an arrow.

Fig. 3. Maximum size of ratio completed on a progressive-ratio schedule, as a function of percentage body weight. Subject 1 was tested at 75% then 100% then again at 75%. Note the different order of percentage body-weight values on the *x* axis.

lever pressing that was reinforced by access to a free-turning running wheel. The persistence of responding on the progressive-ratio schedule increased as deprivation became more severe, but then decreased at the most severe levels of deprivation, suggesting an inverted-U function.

One interpretation of these results is that the reinforcing effectiveness of wheel running is an increasing or inverted-U function of food deprivation. There are, however, other possible interpretations that should be mentioned and that, if correct, would lead to inconsistent results with other methods used to assess reinforcer effectiveness. For example, the changes in the amount of lever pressing (i.e., maximum size of ratio completed) might be a manifestation of changes in overall activity due to

Fig. 4. The total number of lever presses per test session plotted as a function of food deprivation (i.e., percentage body weight).

food deprivation rather than an indication that the reinforcing value of running has changed. If so, an operant such as standing still might not show the same effect as found here. Relatedly, the down-turn of the function at the most severe deprivation level could have resulted from a general debilitation rather than from a specific decline in the effectiveness of wheel running as reinforcement. Finally, it is unclear whether the effects of food deprivation are specific to running.

The results of the progressive-ratio tech-

Table 3

Total number of responses emitted and highest ratio completed (in parentheses). For order of exposure to level of deprivation, see Figures 2 and 3.

Subject	Percentage body weight				
	100	85	75	70	65
1	881 (55)		1,567 (70)		
2	387 (35)		1,882 (80)		
	639 (45)		1,798 (75)		
3	1,507 (70)	1,584 (70)	2,125 (85)	1,300 (65)	
4	1,725 (75)	2,206 (85)	2,870 (95)	2,485 (90)	
5	565 (40)	982 (55)	1,203 (60)	1,439 (70)	781 (50)
6	660 (45)		748 (50)		
7	379 (35)		639 (45)		
8	246 (25)		400 (35)		
9	277 (30)		437 (35)		

Note: Subjects 1 and 2 were exposed to an A-B-A design and the second sets of values represent the return to baseline.

nique are most easily interpreted as indicating ordinal differences in reinforcement effectiveness when it can be assumed that the reinforcement effectiveness of the event being tested remains constant over the duration of the test session. However, if reinforcement effectiveness is declining during the test session as a function of exposure to the reinforcer (i.e., satiation), then the "giving-up" point is confounded by both satiation effects and average reinforcement effectiveness. This complication is most troublesome if satiation proceeds at different rates under the different conditions of interest. If satiation had proceeded at different rates, the results might have been different if a more rapidly increasing progressive schedule had been used.

The reinforcing effectiveness of wheel running could also be indexed by postreinforcement pauses (PRP). The mean PRPs were calculated for the initial three ratio sizes (5, 10, and 15) inasmuch as satiation would be minimal for these early ratios. This measure turned out not to be helpful, however, because mean pause durations were not systematically related to the level of food deprivation. Informal observation of the animals' behavior suggested that there was no systematic relationship between the first response that defined the PRP and the subsequent run of responses. Responses occurred in "bursts" rather than in the break-and-run pattern that is typically observed with fixed-ratio schedules.

Experiment 2 was designed to provide converging evidence about reinforcement effectiveness by comparing the ordering of maximum ratio values obtained by a progressive-ratio schedule with the ordering of responses rates generated by a variable-interval schedule.

EXPERIMENT 2

The results of Experiment 1 suggested that food deprivation (up to a point) was an establishing operation that increased the reinforcement effectiveness of wheel running. Experiment 2 was designed to investigate the possible effect of satiation for wheel running on the effectiveness of food reinforcement.

Subjects

Subjects were 4 male Sprague-Dawley rats obtained from the University's animal colony. Animals were 45 days old and were kept un-

der continuous light conditions in a room with a temperature of 20 ± 2 degrees Celsius.

Apparatus

Two running wheels (Wahmann Co.), one free to turn and the other locked, were used. Also, a Wahmann activity wheel was modified so that it would turn when a motorized metal shaft was rotated by a Superior #M093 stepping motor. Wheel speed was programmed by electronic logic and could be set to several target speeds. Target speed was achieved within 45 s of the command by slowly increasing the wheel revolutions (details in Finley, 1984).

A standard operant-conditioning chamber equipped with a Davis 45-mg pellet feeder, houselight, and response lever was placed inside a sound attenuating enclosure. The enclosure was equipped with an air-circulating fan that also provided masking noise. Coulbourn Instruments programming and recording equipment was used along with a Gerbrands cumulative recorder. The control and recording apparatus was situated in a room separated from the experimental rooms.

General Procedure

All subjects were maintained on standard Lab Blox (Allied Mills) rat chow, with free access to water. Body weights were measured daily for 5 days, and then the animals were reduced to 80% of their free-feeding weights. Next, lever pressing was shaped by reinforcing successive approximations with delivery of food pellets, and in an additional day's session, each press produced a pellet (60 reinforcers). This was followed by two sessions on a variable-interval (VI) 10-s schedule. Finally, the animals were given 18 sessions on a VI 30-s food-reinforcement schedule. Daily sessions were terminated when 60 pellets had been delivered, and sessions occurred on each day of the week. After 18 sessions, all animals' responding had become stable. Stability was assessed by inspection of the cumulative records for trends and by assessing trends and variability in response rates over sessions. When response rates varied less than 10% over five consecutive sessions and when local variation was judged to be small, the stability criterion was achieved. At this point, animals were placed in their home cages and given free access to food and water for 16 days.

After this body-weight recovery period, animals were given free access to food in the

home cages and were given 18 daily sessions on the VI 30-s schedule with food as the reinforcer. This was done in order to determine the baseline response rate for free-feeding animals. Sessions were terminated after 60 pellets or 1 hr, whichever occurred first. Next, the reinforcement effectiveness of food was evaluated by two procedures.

Progressive-Ratio Procedure

The rats were tested on a progressive-ratio schedule similar to that used in Experiment 1. Twenty hours before an animal was to be exposed to the progressive-ratio procedure, it was removed from its home cage and was placed for 19 hr in a Wahmann running wheel with an attached side cage. Water was provided in the side cage but food was not available. During the 19-hr period, the wheel was either locked or free to turn, depending on the experimental condition. Subjects 10 and 20 were first given the locked-wheel condition and next exposed to the open wheel; Rats 30 and 40 were initially given the open-wheel and then the locked-wheel condition. After the exposure to the wheel (locked or open), the animal was returned to its home cage for a 1-hr rest period during which food still was not available. At the end of this hour, the progressive-ratio test session was begun. Thus, animals had been deprived of food for 20 hr at the start of each test regardless of the wheel condition.

To begin the test session, the animal was moved to the experimental room and was placed in the operant chamber; lever presses produced 45-mg food pellets. The progressive ratio started at a value of 5 and was increased by increments of 10 after each food pellet. The test session was terminated if the animal did not finish a ratio requirement within 1 hr of its initiation or after 8 hr in the session, whichever occurred first. This more rapid increase in the progression (compared with that used in Experiment 1) was employed to magnify differences resulting from locked- versus open-wheel conditions. If the ratio had been incremented by five and held for three completions, as in Experiment 1, the animals might have continued lever pressing throughout the session, which would have obscured the effects of wheel running. The dependent variable was the total number of food-reinforced lever presses for the test session.

Variable-Interval Procedure

After the progressive-ratio test, subjects were returned to their home cages and given free access to food for 16 days. In order to establish baselines for the VI test procedure, the animals were food deprived for 20 hr and then exposed to a procedure in which lever presses could produce food according to a VI 30-s schedule. Following each of the VI sessions, subjects were given free access to food for 24 hr, were again food deprived for 20 hr, and were again exposed to the VI schedule. This alternation continued until stable response rates were established on the VI schedule.

In order to assess the effects of wheel running on VI-schedule performance, animals were now given the same procedure as described above, consisting of 19 hr in either a locked or an open wheel plus 1 hr in the home cage. The order of presentation (locked or open) was again counterbalanced: Subjects 10 and 20 were initially given the locked condition followed by open wheel and Subjects 30 and 40 received the reverse order. After the 1-hr home-cage rest period, the rat was placed in the test chamber in which lever pressing produced food according to a VI 30-s schedule. The session was terminated after 60 reinforcers had been obtained or when any inter-reinforcement interval exceeded 1 hr. The dependent variable was rate of lever pressing.

Forced-Running Procedure

Subject 40 did not run during the open-wheel conditions preceding either the incrementing-FR procedure or the VI test session. In order to assess the effect of prior wheel running for this animal, the motorized wheel was used the next day to force running. Inasmuch as rats that ran completed between 600 and 900 turns on the wheel during the 19 hr and did this in four or five bouts of running, the inactive rat was given four bouts of running that totaled 750 wheel turns (a value that was between the minimum and maximum number of wheel turns for active rats). Bouts of running at 5 rpm were scheduled as follows: 200 revolutions at 10:30 a.m., 200 revolutions at 2:00 p.m., 150 revolutions at 7:00 p.m., and 200 revolutions at 7:00 a.m. Following this, the rat was returned to its home cage (no food) and at 10:00 a.m. was tested on the VI 30-s food-reinforcement schedule. Food deprivation was continued

Fig. 5. Total number of lever presses on a progressive-ratio schedule of reinforcement with food, as a function of locked- or open-wheel exposure. Subject 40 did not run on the open wheel and was exposed to the forced-running procedure.

during the day of forced activity (both during the running bout and in the home cage between bouts). Thus, the data for this subject reflect 44-hr periods of food deprivation rather than the 20 hr of deprivation received by other subjects.

RESULTS

Wheel Running

With the exception of Subject 4, the animals ran between 600 and 900 revolutions in the wheel during the 19 hr of open wheel. Typically, most running occurred just after the animal was placed in the wheel and then again in the middle of the 19-hr period. Relatively little wheel running occurred during the last 4 hr of open wheel.¹

Progressive-Ratio Procedure

Figure 5 and Table 4 show that (for Subjects 10, 20, and 30) the amount of food-reinforced lever pressing and the size of completed ratio were smaller when the animals had had an opportunity to run during the previous 20 hr than when they had not been able to run. The decline in lever pressing is surprising given the seemingly moderate amount of wheel

running. However, the amount of running must be judged relative to these animals' sedentary history. Apparently, this change in level of activity is significant for these animals.

For Subject 40, in contrast, access to a free-turning wheel prior to the test session did not produce a decline in lever pressing. In fact, somewhat more food-reinforced lever pressing occurred following the 19 hr of free wheel than following exposure to the locked wheel. This apparent anomaly can be understood inasmuch as the animal did not run during the open-wheel period. Consistent with this interpretation, when Subject 40 was forced to run for 750 wheel turns, the total number of lever presses declined, suggesting that forced running is similar to self-initiated running in its effect on food-reinforced lever pressing. That Subject 40 made approximately twice as many presses as the other animals following forced running can be attributed to two factors. When tested on the progressive-ratio schedule, this animal always emitted substantially more food-reinforced responses than did the other subjects. Also, this subject had been deprived of food for 44 hr when tested following the forced running procedure, whereas the other subjects were tested after 20 hr of food deprivation.

Variable-Interval Procedure

The major results of the VI procedure are portrayed in Figure 6, which shows the cumulative record from the last session of the condition indicated, and in Table 5, which shows those same rates in numerical form. Not surprisingly, response rates were substantially

Table 4

Total number of lever presses emitted for food and highest ratio completed (in parentheses) for subjects exposed to the locked-, open-wheel, and forced conditions. See Figure 5 for order of exposure to the conditions.

Subject	Condition		
	Wheel locked	Wheel open	Forced
10	212 (60)	11 (10)	
20	241 (60)	25 (10)	
30	200 (50)	38 (20)	
40	452 (90)	510 (90)	112 (40)

¹ Cumulative records of wheel running for Subjects 10, 20, and 30 are available upon request.

Fig. 6. Cumulative records for variable-interval 30-s food reinforcement. Records are presented for 80% deprivation, free access to food, 20-hr deprivation, 20-hr deprivation while in the locked-wheel apparatus, and 20-hr deprivation while in the open-wheel apparatus. Subject 40 did not run while in the open wheel and was exposed to the forced-running procedure.

higher when animals were food deprived than when they were not. Nonetheless, it is interesting that animals continued to respond even when they had free access to food in their home cages. These comparisons serve as useful reference points for the experimental manipulation (locked vs. open wheel), because they show the range in variation in response

rate attributable to various levels of food deprivation.

When animals had been placed in the locked wheel and were food deprived for 20 hr, rates of responding were similar to those obtained after 20 hr of food deprivation in the home cage, suggesting that mere placement in a wheel does not effect subsequent food-rein-

Table 5

Responses per minute on VI 30-s schedule of food reinforcement by experimental condition.

Subject	Condition				
	Home cage 80% depriv.	Home cage ad lib	Home cage 20 hr depriv.	Locked wheel 20 hr depriv.	Open wheel 20 hr depriv.
10	40.2	7.8	25.0	27.0	3.0
20	79.8	17.4	29.2	37.4	18.0
30	32.4	19.8	38.0	41.0	27.0
40	42.0	1.2	37.1	39.6	3.6

forced lever pressing. In contrast, being placed in the open-wheel environment for 19 of the 20 hr prior to the test session substantially reduced the rate of lever pressing maintained by the VI 30-s schedule of food reinforcement.

The response rates in Table 5 were calculated for the entire session and include any long pauses that occurred. Consequently, these overall rates possibly exaggerate differences between locked- and open-wheel conditions. It is of interest, therefore, to compare response rates during the early portion of the session when long pauses seldom occurred. The comparison is difficult to interpret, however, because there appears to be a "warm-up" effect early in the session (see Figure 6). Nonetheless, cumulative records show reduced local rates of responding for the open-wheel condition even after the warm-up period.

Subject 40 again failed to run during the 20 hr prior to the VI test session, and so, again, he was required to run in the motorized wheel (see above). Forced running reduced the overall rate of lever pressing from 39.6 (locked wheel) to 3.6 (open wheel) rsp/min for this subject. Inspection of the cumulative record for this rat reveals a substantial decline in local response rate.

DISCUSSION

The results of Experiment 2 indicate that prior running in a wheel reduced the amount of lever pressing on the progressive-ratio schedule and reduced rates of responding on the VI schedule of food reinforcement relative to the level of responding when running was not allowed during the prior 20 hr. Because both procedures provided convergent data, the

case for interpreting these effects as indicating changes in the reinforcing effectiveness of food is strengthened. It still is possible, however, that the effects on lever pressing could be interpreted as manifestations of changes in the overall level of activity resulting from the presence or absence of running during the prior 20 hr. This latter possibility seems unlikely, however, given the small amount of running observed and the 1-hr rest period that preceded the test sessions.

Although the amount of wheel running was less than 1,000 revolutions during the 19-hr period, it was sufficient to reduce the level of food-reinforced responding. Evidently, this amount of running represents a large change when contrasted with a sedentary baseline (cf. Epling & Pierce, 1984). There is some evidence that the decremental effect of prior running on subsequent eating diminishes when animals are given extended exposure to a free-running wheel over a period of days (Tokuyama, Saito, & Okuda, 1982). Thus, if the rats were adapted to regular bouts of running over an extended period of time, the present manipulation might have little or no effect on the effectiveness of food reinforcement.

An interesting comparison can be made between the food-satiation (ad-lib) baseline and the condition preceded by access to an open wheel. Figure 6 shows that the rate and pattern of food-reinforced responding are similar for these two conditions. Apparently, wheel running functions like a satiation operation for food whether or not running is "spontaneous" or forced (see Subject 40).

GENERAL DISCUSSION

The results of these experiments suggest that food deprivation increases the reinforcement effectiveness of wheel running. Also, satiation, by spontaneous or forced activity in a running wheel, decreases the effectiveness of food reinforcement. Thus, the two experiments suggest that deprivation-satiation operations with respect to one event alter the reinforcement effectiveness exerted by another event. Although such effects are well known (cf. phenomena classed under the concept of partial substitution), the range and magnitude of such effects have not been studied as fully as will be required to develop a general understanding of such relationships.

It is not clear why deprivation and satiation operations with respect to food or running function should act reciprocally as establishing operations. It is possible to speculate, however, that the specific interrelationships have a basis in natural selection and so may be species specific (see Epling et al., 1983). Natural selection may have favored those animals that engaged in search patterns under conditions of food scarcity. There are organisms that do not increase running when food is depleted (Cornish & Mrosovsky, 1965); such animals hibernate during seasonal changes that reduce food supply. For these animals, a reciprocal relationship between eating and running would not be expected.

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Received March 4, 1985

Final acceptance April 29, 1986