

RUNNING AND DRINKING BY RATS OUTSIDE THE SCHEDULE SESSION
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ABSTRACT

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Two experiments measured the effects of a contingency schedule relating running and eating on the behavior of rats during an "experimental hour" and during two hours before and afterwards. The behaviors recorded during the surrounding hours were drinking and perching (Experiment 1) and running, drinking and perching (Experiment 2). The temporal pattern of drinking in both experiments was unaffected by changes in conditions during the experimental hour. However, drinking prior to the experimental hour in Experiment 2 was less than in Experiment 1 probably due to competition from wheel running. Rats showed unreliable patterns of perching in both experiments. Finally, running increased both within and outside the experimental hour during the schedule conditions. The increase in wheel running surrounding the schedule hour may represent a combination of species-typical foraging responses and the failure of stimulus control of instrumental behavior. These data suggest that behavior regulation and optimality theories may need to consider the species-typical mechanisms and stimulus control necessary for animals to integrate behavior over time.

INTRODUCTION

Laboratory studies of schedule performance usually focus on an animal's responding during a relatively brief contingency session, typically lasting an hour or less. Yet in the animal's selection environment such a discrete contingency period may affect a broad range of "surrounding" behavior, and these effects can be as important as the more localized effects of the contingency schedule in determining survival. From the standpoint of the animal's ecology, responding during a contingency session reveals only a part of the effects of the schedule.

Though learning researchers generally have not been concerned with changes in the matrix of responding surrounding a contingency session, a number of laboratory studies have shown that a general constraint, such as a restricted period of food availability, has substantial effects on the organization of behavior preceding and following access to food (Bolles & Moot, 1973; Boulos & Terman, 1980; Kambach, 1966; Palya & Zacny, 1980; Richter, 1927; Shettleworth, 1975). For instance, pigeons flapped their wings and paced about the home cage just before a restricted period of feeding, and showed substantial amounts of stereotyped, object-directed pecking for two to three hours afterwards (Palya & Zacny, 1980). Bolles and Moot (1973) and Richter (1927) reported marked increases in running and general activity by rats just before feeding. On the other hand, Barnett, Dickson, Marples and Rahda (1978) found that wild rats regularly explored unbaited arms of a 4-armed residential maze following feeding bouts. Shettleworth (1975)

found that behaviors of hamsters such as scabble, dig and locomotion increased before feeding while scent marking and grooming decreased.

A general purpose of these experiments was to move in a modest way toward an ecological view of the effects of a contingency schedule by examining behavior for two hours on either side of a one hour contingency session (i.e., the "surround" vs. the "experimental hour"). A second purpose of these experiments was to determine the degree to which animals regulated their total behavior in adjusting to the imposition of a schedule. Specifically, if food must be earned under a schedule, does the animal decrease its behavior preceding and following the schedule to compensate for the cost of earning the food under the schedule?

The ability to integrate behavior over time has relevance to theories of optimal foraging (Krebs, 1978; Pyke, Pulliam & Charnov, 1977) as well as to more general behavior regulation theories of learned performance (e.g., Staddon, 1979; Timberlake, 1980; 1984). For example, some foraging studies appear to support the possibility that animals can integrate behavior across days or even months (e.g. Belovsky, 1978). However, a recent laboratory study has suggested that rats cannot appropriately inhibit their foraging behavior in anticipation of food more than an hour distant (Timberlake, 1984).

Experiment 1 established the temporal distribution of drinking and perching (climbing onto a small platform) before (2 hours) and after (2 hours) an hour long experimental session during which running produced access to food. Experiment 2 employed the same design as Experiment 1 except that wheel running was available before and after as well as during the experimental hour. Access to food again was confined to the experimental hour.

EXPERIMENT 1

The purposes of Experiment 1 were to determine whether (a) responses such as drinking and perching showed reliable distributions surrounding the experimental hour, (b) these patterns changed when a schedule relating running to eating was imposed within the experimental hour, and (c) the "surround" paradigm altered the typical effects of a contingency schedule during the experimental hour.

The conditions during the experimental hour included free baseline, contingency (a schedule relating running and eating), and intermittent access. The intermittent access phase was designed to measure the effects of the contingency schedule that could be attributed simply to constraint on the temporal pattern and amount of eating.

METHODS

Subjects. The subjects were 4 female Sprague-Dawley rats. Two rats were 4 months of age and two were 8 months of age at the beginning of the experiment. All rats had previous experience with contingency schedules relating running and eating. Animals were housed individually and deprived of access to food and water in the home cage. One animal in each experiment required supplemental feeding in the home cage every fourth or fifth day to maintain 80% of free feeding weight. Animals were maintained on a 12:12 light-dark cycle throughout the experiment.

Apparatus. Each of the four running-wheel apparatuses was contained in a

large sound-attenuating chamber illuminated by a 7.5-W light bulb. Masking noise was provided by a ventilating fan. Each apparatus consisted of an Acme running wheel (35 cm diameter) mounted by an axle to an angle iron frame. The wheel rotated freely unless stopped by two solenoid operated brakes contacting either side of the front rim of the wheel. A piece of clear Plexiglas confined the animal to the wheel. A square (10 cm x 10 cm) was cut in the Plexiglas, and water and food receptacles were mounted in the opening 5 cm above the bottom of the wheel. The water receptacle consisted of a 3 cm x 4 cm stainless steel tray with a 1 cm diameter recessed well centered in the tray. Water was delivered by a solenoid operated valve that replenished the well with .05 ml of water when the animal emptied it.

Pellets were delivered, as programmed, to a 3 cm x 4 cm x 2 cm deep "V" shaped food tray. Removal of pellets was sensed by a light-emitting-diode beam across the length of the food tray. A 5 cm x 9 cm platform "perch" was located over the wheel axle 20 cm above the base of the wheel. A Texas Instruments 990/10 computer recorded the frequency and duration of eating (.095 g Noyes pellets), drinking (.05 ml drops of water), running (complete wheel turns) and perching (depression of the perch).

Procedure. Rats were placed in the apparatus for five hours at about 11:00 p.m. daily. Drinking was restricted to the first and last two hours. Eating and running were restricted to hour 3 of testing (the experimental hour). The conditions during the experimental hour varied through four phases. Animals continued in each phase for about 25 days. In phase 1 (baseline), eating and running were freely available. In phase 2 (contingency) a schedule ratio relating running and eating was imposed. The schedule ratio satisfied the condition of response deprivation (Timberlake & Allison, 1974) and was initially calculated as the baseline duration of running + 300 seconds/baseline duration of eating. The resulting ratio of durations was then converted to a ratio of response frequencies by dividing the average time per response (during baseline) into the duration value for each response in the schedule ratio. Reciprocal schedules were used under which animals had access to only one response at a time, and access to the alternate response was contingent upon completion of the number of responses determined by the schedule ratio. Each response access represented about 5% of the total frequency determined by the ratio calculated above.

In phase 3 (intermittent access) food pellets were presented independent of the animal's behavior. The frequency and temporal distribution of pellet delivery was yoked to the temporal pattern of earned pellets during the contingency phase. This procedure was designed to assess the noncontingent effects of intermittent food presentations on running during the contingency phase (Timberlake & Wozny, 1979). Phase 4 was a return to the baseline condition.

Scores for each animal represented the median frequency or duration of a response across the last five days of each phase of testing. Statistical analyses that compared baseline and contingency were performed separately from analyses that compared contingency and intermittent access phases.

RESULTS AND DISCUSSION

The data clearly showed an increased number of wheel turns during the contingency phase. Animals ran more during contingency ($\bar{M} = 427$, S.E. = 83) than first baseline ($\bar{M} = 191$, S.E. = 84), $t(3) = 9.16$, $p < .005$, or second baseline ($\bar{M} = 84$, S.E. = 16), $t(3) = 3.65$, $p < .05$. Animals also ran more during contingency than intermittent access ($\bar{M} = 270$, S.E. = 102), $t(3) = 3.72$, $p < .025$. Thus, the "surround" procedure does not interfere with the basic effects of the schedule on instrumental behavior usually observed in studies of learned performance (e.g., Timberlake & Wozny, 1979).

Table 1

Mean Drinks (.05 ml each) as a Function of Hour and Phase of Testing in Experiments 1 and 2 - standard error in parentheses.

Experiment 1	Hour			
	1	2	4	5
Phase				
Baselines	93 (27)	34 (14)	130 (27)	11 (5)
Contingency	95 (32)	32 (15)	138 (37)	23 (13)
Int. Access	86 (25)	26 (15)	104 (16)	19 (17)

Experiment 2	Hour			
Phase	1	2	4	5
Baselines	29 (7)	4 (2)	168 (40)	24 (2)
Contingency	20 (9)	2 (1)	222 (119)	11 (5)
Int. Access	31 (9)	4 (1)	193 (77)	25 (5)

Animals showed a reliable temporal pattern of drinking surrounding the experimental hour. Table 1 shows that animals drank more during hour 1 than hour 2, $F(1, 3) = 13.92$ and 22.43 , $p's < .05$. A similar decrease in drinking occurred between hour 4 and 5, $F(1, 3) = 25.32$ and 38.05 , $p's < .05$. There were no significant differences in the amount of drinking before and after the experimental hour. This pattern was unaffected by the imposition of a schedule constraint between running and eating. Animals drank less during intermittent access than baselines, $F(1, 3) = 12.96$, $p < .05$, but maintained the same basic pattern observed in the other phases.

There was substantial variability between animals in the temporal pattern of perching across hours and phases of testing. Table 2 shows mean seconds on the perch across phases. There were no reliable effects of either the hour or phase of testing on perch time. The only reliable effect was that animals spent less time on the perch during the experimental hour (hour 3) than the average of hours outside hour 3, $t(3) = 1.96$, $p < .05$.

EXPERIMENT 2

Experiment 2 used the same "surround" paradigm as Experiment 1, but added wheel running as a possible response outside the experimental hour. This procedure seemed more analogous to natural circumstances in which animals may move about the environment freely, but food availability is restricted to particular locations and/or times. The availability of running may affect the distributions of drinking and perching found in Experiment 1, and running itself may vary as a function of its role during the experimental hour.

Table 2

Mean Seconds on Perch Across Hours of Testing in Experiments 1 and 2 - standard error in parentheses.

	Hour				
	1	2	3	4	5
Exp. 1	405 (244)	932 (338)	76 (29)	169 (80)	257 (158)
Exp. 2	472 (74)	434 (138)	29 (6)	458 (65)	605 (147)

Previous reports indicate that rats increase running in anticipation of a restricted period of food availability (Bolles & Moot, 1973; Boulos & Terman, 1980; Richter, 1927). Such an effect might have been selected for in the animal's evolutionary history because increased activity in the presence of feeding cues increased the probability of finding food. On this basis animals should run more before than after the experimental session during all conditions and this basic effect may be enhanced by the schedule relation between running and eating.

However, various theories of foraging behavior (Krebs, 1978; Pyke, et al., 1977) and behavior regulation (e.g., Rachlin, Battalia, Kagel & Green, 1981; Staddon, 1983; Timberlake, 1984) suggest that animals should minimize or at least decrease ineffective appetitive behavior to decrease overall costs of foraging. In this view, increased running to obtain food during the experimental hour should not be accompanied by increased running outside. One might even predict decreased running outside to compensate for the increase in running within the experimental hour.

METHODS

Subjects. Subjects were 8 female Sprague-Dawley rats. Ages, housing conditions and experimental history were the same as described for the 4 rats used in Experiment 1.

Apparatus. The apparatus described in Experiment 1 was used in Experiment 2.

Procedure. The four phases of testing in Experiment 2 were the same as those described for Experiment 1 except that running was available during all five hours of testing. Scores were calculated and analyzed as described in Experiment 1.

RESULTS AND DISCUSSION

Figure 1 shows that, during the schedule phases, rats increased running both during and outside the experimental hour. During the experimental hour animals ran more during contingency than baselines, $t(7) = 8.08$, and more during intermittent access than contingency, $t(7) = 2.01$, $p < .05$. The latter result was unexpected, and it appeared that the animals failed to discriminate response-independent intermittent food presentations from response-contingent presentations. They behaved as though the intermittent presentation condition was a variable schedule of reinforcement and exhibited higher rates of responding than under the fixed schedule (Schwartz, 1978). That animals in Experiment 1 did not

show this effect suggests that access to the running wheel outside the experimental hour may have interfered with discrimination between food-related and food-independent running.

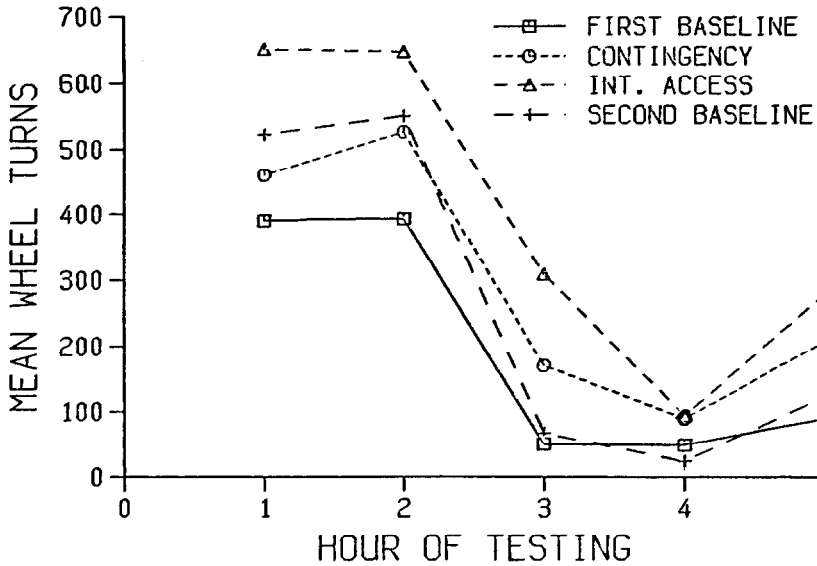


Figure 1. Mean wheel turns during hours 1 through 5 for each phase of testing in Experiment 2. Access to food was confined to hour 3. See text for description of conditions for each phase.

Figure 1 also indicates that there were substantial increases in running outside the experimental hour during schedule conditions. Before the experimental hour, rats ran more during contingency than in the first baseline, $t(7) = 1.81$, $p < .06$ but not the second baseline. After the experimental hour, rats also ran more during contingency than baselines, $F(1, 7) = 6.11$, $p < .05$ and showed a significant increase in running between hours 4 and 5, $F(1, 7) = 5.56$, $p < .05$. Before the experimental hour, rats ran more during intermittent access than contingency, $F(1, 7) = 31.00$, $p < .001$, but there were no differences in running between intermittent access and contingency after the experimental hour. Also, across phases it can be seen that animals ran substantially more before than after the experimental hour.

The increase in running both before and after the experimental hour during

the schedule was unexpected. Though an anticipatory view might explain the increase in running before the schedule hour, it does not predict increased running after the schedule hour. An optimality/behavior regulation view suggests neither an increase before nor after the schedule hour.

Table 1 shows the temporal pattern of drinking in Experiment 2. Animals drank more during hour 1 than hour 2, $F(1, 7) = 31.97$, $p < .001$ and more during hour 4 than hour 5, $F(1, 7) = 4.88$, $p < .05$. The temporal pattern of drinking differed from Experiment 1 in that animals showed less drinking before than after the experimental hour whereas there was no difference in drinking before and after the experimental hour in Experiment 1. Thus, it appeared that running successfully competed with initial drinking in Experiment 2. Animals appear to delay some of their drinking when given opportunity to engage in locomotor behavior before feeding.

As in Experiment 1, animals showed no consistent pattern of perching except for a decrease in perch time during hour 3 relative to the remaining hours, $t(7) = 2.38$, $p < .05$. Table 2 shows mean seconds perch time for hours 1 through 5. The data were averaged across phases of testing because there were no differences between baseline and schedule phases.

GENERAL DISCUSSION

The present experiments showed reliable patterns of running and drinking, though not perching, by rats before and after an experimental hour in which food was available. The temporal patterns of drinking and running were unaffected by the presence of schedule constraints relating running and eating during the experimental hour. However, the schedule produced an increase in running both before and after the experimental hour.

This finding seems inconsistent with general optimality or behavior regulation theories applied to feeding behavior. Animals did not limit running surrounding an experimental hour in which running produced access to food. Rather, animals showed substantial increases in running before and after the schedule hour. Thus, rats have tendencies to look for and be active in the presence of cues associated with a single period of food availability even considerably prior to and following the delivery of food. This finding may represent species-typical anticipatory (Bolles & Moot, 1973; Richter, 1927) and/or post-feeding exploratory behavior (Barnett et al., 1978) that is enhanced by the schedule relation.

Some preliminary additional data suggest that a part of the schedule induced running in Experiment 2 was due to animals' failure to discriminate the experimental hour from the surrounding hours. Two animals from Experiment 2 were provided with a loud tone during the experimental hour as an extra cue to distinguish it from the surrounding hours. These animals showed much less running during intermittent access prior to the experimental hour than in Experiment 2. However, they still showed a slight increase in running before the experi-

mental hour during contingency as compared to baseline.

Considering other recent data (Timberlake, 1984; Melcer & Timberlake, 1985) it may be useful to view foraging behavior as the result of a variety of behavioral mechanisms that suit the animals for a specific range of environments and food distributions. When the animal's ability to time and integrate behavior across hours is tested carefully it may be found to be restricted by specific environmental circumstances. Such restrictions on the animal's ability to integrate information about response and reward may also apply to behavior regulation and compensation theories.

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