System-Specific Differences in Behavior Regulation: Overrunning and Underdrinking in Molar Nondepriving Schedules

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In two experiments we tested the molar regulation prediction that animals adjust schedule performance to reduce deviations from baseline response totals. Both experiments constrained the baseline drink-burst length under molar nondepriving schedules but allowed rats to continue running without drinking. In Experiment 1, rats were required to run in order to drink. In Experiment 2, water was delivered independently of running by fixed-time (FT) schedules. Under the run-to-drink contingency, rats exceeded their baseline amounts of running (overrunning) but failed to maintain their baseline water intake (underdrinking). The total amount of running that did not lead to drinking approximated baseline running. Under the FT schedules, rats again underdrank, but total running approximated baseline. These results do not support previous studies that have shown molar equilibrium effects under nondepriving reciprocal schedules. We conclude that (a) contingent running may not substitute for independent running; (b) intermittent access to water reduces the total instigation for drinking; (c) molar regulation differs under reciprocal and nonreciprocal schedules; and (d) more dynamic, system-specific regulatory models need to be developed.

Molar behavior regulation models (Allison, 1976, 1980; Hanson & Timberlake, 1983; Staddon, 1979; Timberlake, 1980, 1984; Timberlake & Allison, 1974) assume that animals adjust schedule performance in order to approach baseline levels of instrumental and contingent responding. Thus, these molar models predict that total baseline responding should be maintained when the terms of the schedule are nondepriving at the molar level (see Timberlake, 1980). In effect, these models assume that motivational systems regulate deviations from response totals rather than from local response characteristics (e.g., burst and interburst durations, temporal distributions of responding—see Allison, Moore, Gawley, Mondloch, & Mondloch, 1986; Dunham, 1977; Gawley, Timberlake, & Lucas, 1986; Premack, 1971; and Timberlake, 1980, 1984, for further discussion of local and molar regulatory processes).

However, Gawley et al. (1986) found that both local and molar response characteristics were defended under molar nondepriving schedules that constrained the baseline drink-burst length. At the molar level, rats maintained their overall amount of baseline water intake and wheel running under all degrees of drink-burst constraint. But at a more local level, the animals increased their rate of drinking during the first half of the hour session as the drink-burst constraint increased. Further, the relative latencies of wheel-to-drink and drink-to-wheel transitions indicated that the motivation for running was greater than the

motivation for drinking during the last half of the session. These local adjustments in schedule performance formed the basis of the temporal density hypothesis (Gawley et al., 1986). Gawley et al. posited that these local changes were motivated by the tendency to maintain the respective baseline temporal distribution of drinking and running (see also Mook & Dreifuss, 1986; Premack, 1971; Terhune, 1978).

However, the tendency to maintain both the baseline temporal distributions and response totals may have been affected by the reciprocal schedule. That is, the reciprocal schedule used by Gawley et al. required the rats to run in order to drink, *and* drink in order to run (cf. Premack, 1962). Accordingly, the rats appeared to be more strongly motivated to run in order to drink during the first half of the session, but then appeared to drink in order to run during the last half of the session. The reciprocal contingency, however, may have suppressed running during the later part of the session because an increase in running would have required the rats to exceed baseline water intake. Thus, if the schedules were nonreciprocal (i.e., the schedules did not require the rats to drink in order to run), rats might run more and drink less during the last half of the session. These local changes in responding could therefore produce overrunning and/or underdrinking under nondepriving schedules if the reciprocal contingency were removed.

The purpose of the current research was to determine whether rats would maintain their overall baseline amount of drinking and running under nondepriving and nonreciprocal schedules. As in the Gawley et al. (1986) study, the current experiments constrained the baseline drink-burst length while providing the opportunity for the animals to maintain their total baseline water intake by performing their baseline amount of running (i.e., a molar nondepriving schedule). However, unlike the Gawley et al. study, the current constraints did not require strict alternation between running and drinking. In Ex-

periment 1, drinking was contingent on running, but the animals could continue to run at any point in the session without drinking. In Experiment 2, fixed-time (FT) schedules delivered water at approximately the same local rate at which the animals had earned it in Experiment 1 but independent of any wheel running requirement. Experiment 2, therefore, allowed us to assess the effect of noncontingent intermittent water schedules on wheel running and drinking.

Because the animals had unrestricted and continuous access to the running wheel in both experiments, we could differentiate between two classes of running: (a) running that led to drinking (coupled running) and (b) running that did not lead to drinking (uncoupled running). This distinction allowed us to determine whether coupled running reduced the instigation[1] for uncoupled running. It may be that behaviors, when linked by a contingency schedule, are not instigated by the same factors as they are when expressed independently (i.e., free-baseline). In other words, coupled running may not be a perfect substitute (Allison, 1983; Timberlake, 1979) for baseline (uncoupled) running. In that case, time allocated to coupled running might actually "deprive" the rats of uncoupled running.

Regarding drinking, the current experiments allowed us to determine whether local constraints on drinking patterns affected total water intake in the absence of a reciprocal contingency. A failure to maintain baseline water intake under the current nondepriving schedules would not only raise questions about molar behavior regulation models, but would also, as suggested by the temporal density hypothesis (Gawley et al., 1986, p. 92), question whether deviations from the baseline temporal distribution of drinking accumulate perfectly over time.

General Method

Subjects

The subjects were female Sprague-Dawley albino rats (120 days old) obtained from a local breeding colony at Indiana University. The rats were housed separately with free access to Purina Rat Chow in their home cage and were maintained on a 23-hr water deprivation regimen under a 12-hr/12-hr light/dark cycle. All experimental procedures were conducted during the light phase of the cycle.

Apparatus

The apparatus consisted of four metal boxes containing Acme running wheels (36-cm diameter × 14-cm deep) that were mounted on an axle attached to an angle-iron frame. The animal was confined to the wheel by a Plexiglas wall mounted flush with the iron frame. Movement of the wheel could be stopped by two solenoid-operated brakes that contacted the perimeter of the wheel. As the wheel turned, a metal flag attached to its perimeter interrupted two photobeams (1 cm apart), which allowed us to determine whether the rat was running clockwise or counter-clockwise. Only 360° revolutions of the wheel in the same direction were counted as wheel turns.

The source of water was a small (1 cm in diameter) brass bowl mounted in a recessed opening in the Plexiglas wall 5 cm above the bottom rim of the wheel. Each water presentation consisted of a 0.05-ml volume of water delivered through a 2-mm opening in the bottom of the bowl via a Skinner valve (New Britain, Connecticut). A continuity circuit between the brass bowl and the water detected when the bowl was emptied, that is, the consumption of each 0.05-ml unit of water. Additional water could be delivered within 50 ms after the circuit was

broken. The design of the drinking system thus provided a continuous source of water as the animal drank while controlling intake at a 0.05-ml resolution. Note that the measurement of drinking is not in terms of licks but rather the number of 0.05-ml units of water consumed (20 drinks equals 1 ml of water). The water system was calibrated daily.

Each wheel apparatus was contained in a sound-attenuating chamber illuminated by a 7.5-W bulb located at the top right-hand corner at the back of the chamber. An 80-dB/2000-Hz Sonalert tone source (P. R. Mallory & Co., Indianapolis, Indiana) was located on the top left-hand corner of the iron frame. A ventilation fan located at the back of the chamber just below the light bulb provided masking noise. The chambers were located in a light- and sound-shielded room, and the apparatus was controlled by a TI-990 computer system (Texas Instruments, Austin, Texas) located in an adjacent room. All programed contingencies and data collection were arranged with a 50-ms resolution.

Procedure

One week before the onset of the experiment proper, the subjects' access to water was restricted to 1 hr each day in their home cages. Immediately following this initial deprivation experience, the subjects began the experiment proper, which consisted of 1-hr daily sessions, 7 days a week, segmented into the following four phases:

Phase 1. The first phase of the experiment consisted of a paired-baseline procedure in which the rats had free access to both water and the running wheel in the apparatus for 69 sessions.

In order to establish empirical criteria for the duration of a burst of drinking and running, log survivor functions of interdrink and interrun intervals were examined from six consecutive sessions in the precontingency baseline. A log survivor plot reveals patterns of interresponse times by changes in the slope of the curve (Lehner, 1979). Visual inspection of the log survivor curves of individual subjects showed a marked change in the probability of drinking and running after a pause of 4.2 s and 2.7 s, respectively. On the basis of these criteria, a burst of drinking and running continued until no response occurred within 4.2 s and 2.7 s of the preceding response, respectively (see Gawley et al., 1986). After these burst criteria were established, additional sessions of the precontingency baseline were conducted to determine the average number of drinks per burst.

Phase 2. After the paired-baseline procedure was completed, a single-baseline procedure for drinking and wheel running was conducted. The single-baseline is used to assess the instigation for a behavior in the absence of competition from an alternate behavior. In the single-baseline for drinking, the animals had free access to water but no access to the running wheel either before or during the 1-hr session.

In the single-baseline for running, the animals had free access to the wheel for the entire session, but no access to water during the session. Rather, the animals received their paired-baseline average amount of water 1 hr prior to the session in their home cage. Food was removed from the home cage during this period to prevent the animals from feeding before running. We conducted the single-baseline for running in this manner because most of the running in paired-baseline occurred after drinking.

The single-baseline procedure was conducted for eight consecutive sessions for drinking, and eight consecutive sessions for wheel running. The order of the two single-baseline procedures was counterbalanced across subjects.

Phase 3. The third phase of the experiment consisted of four schedule conditions in which the paired-baseline average number of drinks

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[1] We use the term *instigation* in this article to refer to the combined effects of both the external incentive stimuli and the internal physiological deficits that determine the motivational tendency of the organism in the experimental context.

per burst was constrained to different degrees while the baseline ratio of instrumental to contingent responding was maintained (i.e., nondepriving schedules). Each access to water under the various schedules provided 0.10, 0.25, 1.0, or 1.5 of the baseline average number of drinks per burst.

In Experiment 1, the schedules were nonreciprocal in that they did not require the animal to consume the water earned to continue to run in the wheel. In Experiment 2, FT schedules delivered water independently of wheel running. Thus, in both experiments rats could continue running without drinking at any point in the session. If an animal did not drink all the water as it was made available by the schedules, then the control program stored these "unused" drinks for future consumption (i.e., unlimited hold). For example, if an animal earned 20 drinks but consumed only 10 of these 20 drinks, then the remaining 10 drinks were not lost but rather remained available throughout the session. A 500-ms tone sounded each time that additional drinks became available in both experiments.

The animals were exposed to only one schedule condition during a particular session, and all schedule conditions were in effect for 12 consecutive sessions. Half of the subjects received the schedule conditions in ascending order, and the other half received them in descending order.

If total water intake on a given day was below an animal's baseline average intake, the animal was given the difference 1 hr after the end of the session. This procedure prevented long-term water deficits from occurring during the contingency phase of the experiment.

Phase 4. The final phase of the experiment was a postcontingency paired-baseline procedure in which the animals again had free access to both water and the running wheel for 27 sessions.

Response Measures and Analysis

Coupled and uncoupled running. Coupled running was defined as running that led to drinking, and uncoupled running was defined as running that did not lead to drinking. In Experiment 1, the amount of coupled and uncoupled running was based on the number of drinks earned and drinks consumed in each 10-min bin. If a rat consumed all of the drinks it had earned in a particular bin, we counted all the wheel turns in that bin to be coupled. If a rat did not consume all the drinks earned in a particular 10-min bin, we counted all wheel turns expended in producing these "unused" drinks as uncoupled wheel turns. In effect, uncoupled wheel turns were wheel turns unnecessary to obtain access to the water that was consumed. In Experiment 2, all wheel turns were counted as uncoupled in that they were not necessary to obtain water.

Data analysis of asymptotic performance was based on the last 12-session block for the pre- and postcontingency paired-baselines, and the last 6-session block in the single-baselines and all schedule conditions. Statistical analysis of the data included repeated measures analysis of variance (ANOVA), *t* tests for correlated samples, and Tukey's HSD (honestly significant difference) test for all post hoc multiple comparisons.

Because pre- and postcontingency paired-baseline measures showed no appreciable differences, the baselines were combined to yield an average paired-baseline score. Thus, though both pre- and postcontingency baseline measures are displayed in the figures, only the combined paired-baseline scores were used for statistical tests.

Experiment 1

Behavior regulation studies have frequently used reciprocal schedules to ensure that the ratio of two behaviors remained as close as possible to the programed ratio (e.g., Allison & Timberlake, 1974; Gawley et al., 1986; Mazur, 1975; Tierney, Smith, & Gannon, 1983). However, this cross-coupling of different motivational systems may make it difficult to determine which par-

ticular system is controlling performance at different points in the session because the schedule requires that the expression of one behavior must covary with the expression of the other. Thus, as suggested in Gawley et al. (1986), the expression of the motivation for running during the last half of the hour session might have been constrained because the reciprocal schedule required the rats to drink in order to run.

In the present experiment we repeated the type of constraint on the drink-burst length used by Gawley et al. (1986) while relaxing the restriction on wheel running imposed by the reciprocal contingency. Rats were exposed to four run-to-drink contingencies that differentially constrained their baseline average number of drinks per burst, but all the constraints allowed the rats to run without drinking at any point in the session. Furthermore, all schedule conditions were nondepriving in that rats could earn their total baseline amount of water by maintaining their total baseline amount of wheel running.

From a molar perspective, the total amount of running and drinking should approximate baseline because of the nondepriving nature of the schedules. However, if coupled running (running related to obtaining water) does not reduce the instigation for uncoupled running (running not related to obtaining water), then the total amount of running (coupled + uncoupled) may exceed baseline, even though the schedules are nondepriving.

The local amount of uncoupled running in a 10-min bin may provide some insight into the question of whether deviations from baseline (uncoupled) running accumulate during periods of coupled running. If deviations accumulate, then the local amount of uncoupled running during the later portion of the session should be greater than the local amount of baseline running. Another possibility is that deviations are not accumulated within a session and that uncoupled running during the later portion of a session is driven primarily by the local amount of instigation. This hypothesis would be supported if the local amount of uncoupled running approximated the local amount expressed in baseline during the later portion of the session.

A molar approach also predicts that baseline total water intake should be maintained under nondepriving schedules. On the other hand, the data from Gawley et al. (1986) suggest that local disruption of the baseline temporal distribution of drinking may reduce the total effective instigation for drinking. In this event, total water intake should be less than baseline because the schedules allow the rats to stop drinking at any point in the session without preventing wheel running.

Method

Eight female rats served as subjects. One rat died, leaving 7 subjects in the experiment. Schedule parameters were determined individually for each subject. Tables 1 and 2 show the necessary precontingency paired-baseline measures and schedule parameters.

Results

Running. Figure 1 shows the mean session total wheel turns. Constraint on the baseline average number of drinks per burst produced a marked increase in total wheel turns, $F(5, 30) = 17.52, p < .01$. Post hoc analysis revealed that total wheel turns

Table 1

Mean Measures of Precontingency Paired-Baseline Responding for Individual Subjects in Experiment 1

Rat	Wheel	Wheel SE	Drink	Drink SE	O_i/O_c	Dbst	Dbst SE
2	339.6	22.8	249.8	11.3	1.36	24.97	3.1
3	704.0	47.8	283.1	8.1	2.49	18.07	2.2
4	523.3	60.8	292.0	13.1	1.79	38.49	3.3
5	635.0	41.1	259.4	8.1	2.45	26.15	4.1
6	295.8	17.4	287.5	15.7	1.03	13.69	2.7
9	801.1	19.3	262.1	11.6	3.06	9.17	0.6
11	798.7	41.7	245.0	11.0	3.26	17.49	3.8

Note. Running and drinking measures are reported as means of total session responses. Means were based upon the last 12 sessions of the precontingency paired-baseline. Wheel = total wheel turns; Wheel SE = standard error for total wheel turns; Drink = total drinks; Drink SE – standard error for total drinks; O_i/O_c = baseline ratio of total wheel turns (O_i) to total drinks (O_c); Dbst = mean number of drinks per burst; Dbst SE = standard error for number of drinks per burst.

in all schedule conditions were greater than in either the paired- or single-baselines, but did not vary significantly as a function of the constraint. Total wheel turns in the single- and paired-baseline conditions were not significantly different.

Figure 2A shows the mean wheel turns in each 10-min bin for baselines and total (coupled + uncoupled) wheel turns in each 10-min bin for all schedule conditions. In the paired-baseline condition, wheel running varied significantly within the session, $P(5, 30) = 4.75$, $p < .05$. Post hoc analysis indicated that running in the first 10-min bin was significantly less than in the last five 10-min bins. The local amount of running in the single-baseline condition did not vary significantly within the session, $F(5, 30) = 0.51$, $p > .76$. The suppression of running in the first 10-min bin in the paired-baseline condition was probably caused by the competition from drinking as evidenced by the greater amount of running during the first 10-min bin in the single-baseline condition.

Total wheel turns in each 10-min bin did not vary significantly within the session in any schedule condition, all Fs (5, 30), $ps > .07$. Given that total wheel turns in each 10-min bin did not vary significantly within the session and that there were no significant differences between the overall amounts of running obtained under the four schedules (see Figure 1), the means in each 10-min bin were collapsed across the four sched-

ules in order to compare running in the paired-baseline and the schedules. Total wheel turns in each 10-min bin under schedule constraint were greater than the respective amounts expressed in the paired-baseline condition, all ts (6), $ps < .01$.

Mean coupled and uncoupled wheel turns in each 10-min bin are shown in Figure 2B. Recall that running that led to drinking was defined as coupled running, and running that did not lead to drinking was defined as uncoupled running. Coupled running accounted for nearly all of the running that occurred at the beginning of the session, but then it decreased systematically over the course of the session, all $Fs(5, 30)$, $ps < .05$. Conversely, uncoupled running did not occur at all until the second 10-min bin of the session, and then it progressively increased over the remainder of the session, all $Fs(5, 30)$, $ps < .05$. Post hoc analysis indicated that uncoupled running in the last two 10-min bins was significantly greater than in the first three 10-min bins.

A two-factor within-subject ANOVA was used to analyze paired-baseline running with the collapsed means for uncoupled running under the four schedule conditions. The analysis indicated no significant main effect of condition (baseline vs. schedule), but there was a significant main effect of bin, $F(5,$

Table 2

Schedule Parameters for Individual Subjects in Experiment 1

	Schedules (wheel/drink)			
Rat	BL 1.50	BL 1.00	BL 0.25	BL 0.10
2	50.95/37.46	33.96/24.97	8.49/6.24	3.40/2.50
3	67.50/27.11	44.99/18.07	11.25/4.52	4.51/1.81
4	103.35/57.74	68.90/38.49	17.22/9.62	6.89/3.85
5	96.11/39.23	64.07/26.15	16.02/6.54	6.42/2.62
6	21.16/20.54	14.10/13.69	3.53/3.42	1.41/1.37
9	42.11/13.76	28.06/ 9.17	7.02/2.29	3.06/1.00
11	85.54/26.24	57.02/17.49	14.25/4.37	5.71/1.75

Note. Schedule parameters are reported as the number of wheel turns to the number of drinks under each schedule requirement. BL = burst length ratio.
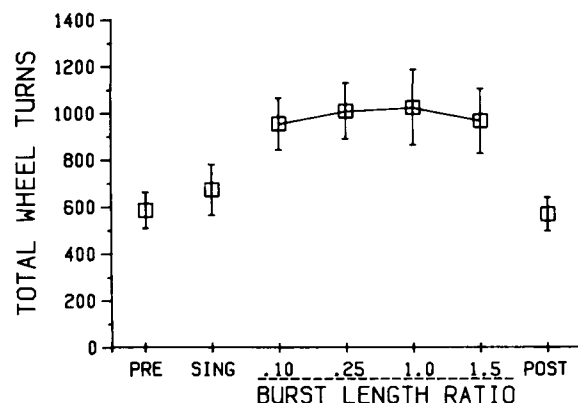

Figure 1. Mean session total wheel turns for Experiment 1. (Vertical bars represent the standard error of the means. PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline.)
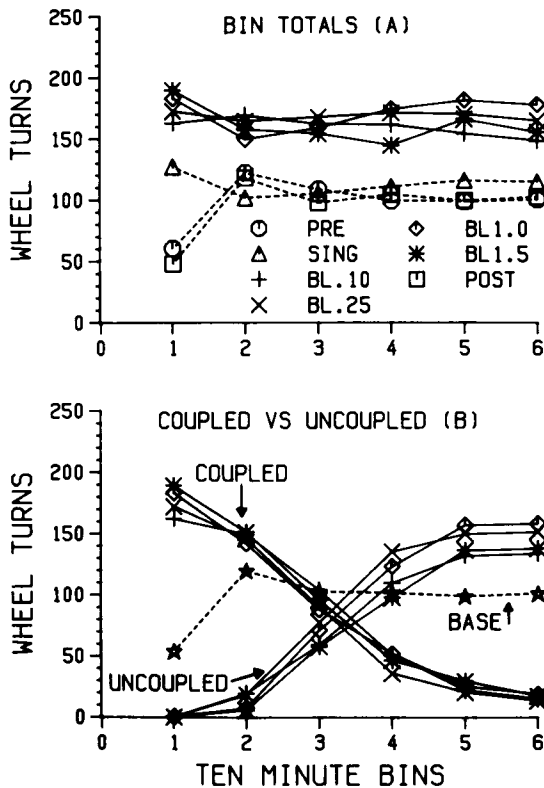
Figure 2. Mean wheel turns for all baselines (dashed lines) and schedule conditions (A) and coupled and uncoupled wheel turns in each 10-min bin (B) in Experiment 1. (PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline; BL = burst length ratio; BASE = combined paired-baseline average.)

30) = 11.18, $p < .05$, and a significant interaction effect, $F(5, 30) = 18.23, p < .05$. Uncoupled running was significantly less than baseline running in the first two 10-min bins, all $Fs(1, 6)$, $ps < .05$, but uncoupled running increased over the remainder of the session. Note that this local increase in uncoupled running resulted in no significant difference between total paired-baseline running and total uncoupled running under the four schedule conditions, $F(1, 6) = 1.01, p > .35$.

Drinking. Figure 3 shows mean session drink totals in 0.05-ml units. Total drinks decreased under all schedule conditions relative to baselines, $F(5, 30) = 13.64, p < .01$. Post hoc analysis indicated that total drinks in all schedule conditions did not vary significantly as a function of the drink-burst constraint. Total drinks in the paired- and single-baselines were not significantly different.

Figure 4 shows how the various schedules affected drinking in 10-min bins within the session. The total number of drinks in each 10-min bin did not vary significantly across the four schedules (Panel A), all $Fs(3, 18), ps > .26$. Thus, the 10-min bin totals were collapsed for comparisons with paired-baseline. In the first 10-min bin, schedule drinks were less than the drinks during the first 10 min in paired-baseline, $t(6) = 19.62, p < .05$, but were greater than baseline drinks over the last five 10-min bins, all $ts(6), ps < .05$. However, this relative increase in drinking over the last five 10-min bins was never of sufficient quantity

to maintain total baseline drinks as shown by the cumulative percent of total baseline drinks in Figure 4B.

Figure 4C shows the mean number of drinks earned versus the number of drinks taken in the four schedule conditions. The data clearly show that the subjects continued to accumulate drinks at a fairly constant rate across the session. However, by the third 10-min bin, the subjects consumed only about 60% of the drinks they earned, and, over the last two 10-min bins, they consumed less than 15% of the drinks earned.

Discussion

The overrunning and underdrinking effects in the current experiment were not consistent with the molar effects obtained under the nondepriving schedules used in the Gawley et al. (1986) study. The key procedural difference between these two studies was the use of a reciprocal contingency. Gawley et al. argued that their rats may have been drinking in order to run during the later portion of the session because of the reciprocal contingency. This contention appears to be supported by the current results in that the rats continued to run without drinking during the later portion of the session even though the overall amount of running was substantially greater than in baseline. It thus appears that, at least for drinking and wheel running over an hour's session, a reciprocal contingency produces a different result than a nonreciprocal contingency.

The overall increase in wheel running may be due to two effects. First, coupled running did not substitute for uncoupled running, so the tendency to run was not reduced by running that occurred in service of drinking. Second, it appears that deviations from the baseline temporal distribution of running accumulated across the early portion of the session when the rats were engaged in coupled running. These deviations summed with the local instigation for uncoupled running during the later portion of the session to produce a total amount of uncoupled running that closely approximated baseline running.

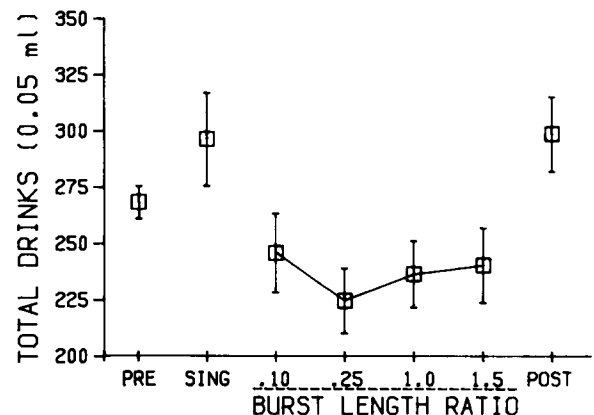The reduction in drinking suggests that deviations from the

Figure 3. Mean session total drinks in 0.05-milliliter units for Experiment 1. (Vertical bars represent the standard error of the means. PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline.)
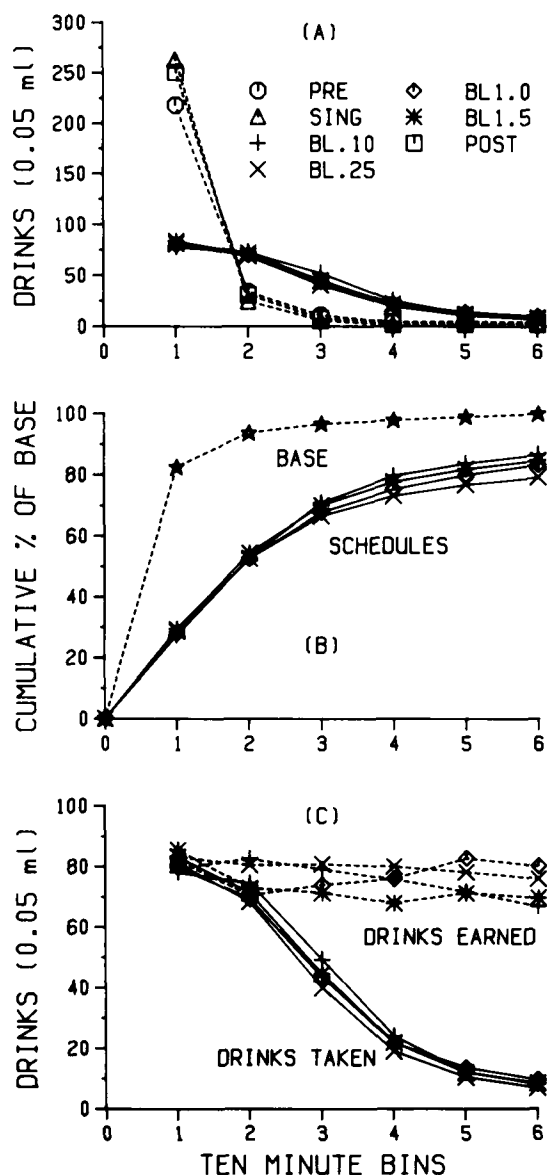
Figure 4. Mean drinks in 0.05-milliliter units in each 10-min bin (A), cumulative percent of total paired-baseline drinks (B), and drinks earned versus drinks taken for all schedule conditions in Experiment 1. (PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline; BL = burst length ratio; BASE = combined paired-baseline average.)

baseline temporal distribution of drinking were not perfectly accumulated over the session. Given no requirement to drink in order to run, the animals essentially stopped drinking after about 30 min. Hence, it appears that local disruptions of the baseline temporal distribution of drinking reduce the total effective instigation for drinking. Although the current constraint of drinking occurred at the level of an individual drink burst, the constraint indirectly perturbed the baseline temporal distribution of drinking. In paired-baseline, 85% of the total water intake occurred within the first 10 min of the session. These results are typical for the temporal distribution of water

intake for deprived rats (Allison et al., 1986; Hatton & Bennett, 1970; Rolls & Rolls, 1982; Gawley et al., 1986). The current constraints reduced this proportion to approximately 25% within the first 10-min bin and forced the rats to consume a larger proportion of water over the remainder of the session. However, even though the local amount of drinking was greater than in baseline over the last 50 min of the session, rats failed to consume enough water to maintain baseline total water intake.

Both the overrunning and underdrinking effects found in the current experiment contradict some of the traditional assumptions of molar behavior regulation models (Allison, 1976; Hanson & Timberlake, 1983; Staddon, 1979; Timberlake, 1980; Timberlake & Allison, 1974). However, the data suggest some form of regulation in that (a) the total amount of uncoupled running closely approximated baseline, and (b) the reduction in total water intake was approximately the same under all four schedule conditions. Nevertheless, there are several plausible alternative explanations, some of them nonregulatory, that could account for the overrunning and underdrinking effects. These alternative explanations are examined in the next experiment.

Experiment 2

One explanation for the overrunning effect in Experiment 1 is that it may have been caused by nonspecific motivational factors associated with intermittent schedules. For example, it is well known that intermittent food schedules produce an increase in general activity in rats (e.g., Falk, 1971, 1983; Roper, 1980, 1981; Staddon & Ayres, 1975). Schedule-induced running under intermittent food and water schedules also has been reported by some authors (King, 1974; Levitsky & Collier, 1968; Lucas, Timberlake, & Gawley, in press; but see Staddon, 1977, and Roper, 1981, for criticisms of the concept of schedule-induced running).

The underdrinking effect also requires consideration of at least two alternative explanations. One explanation is that the reduction in drinking was caused by competition with wheel running during the later portion of the session. That is, the accumulated deviations from baseline running in Experiment 1 might have competed with drinking during the last half of the session. It could be that rats would maintain baseline total water intake under the current constraints if competition from wheel running was reduced during the later portion of the session.

The reduction in drinking might also be explained as a substitution effect (Allison, 1983; Timberlake, 1979). When coupled running increased, total drinking decreased, as if coupled running and drinking were substitutes. Specifically, a portion of the total instigation for drinking may have been expressed in coupled wheel running. A substitution hypothesis predicts that the reduction in drinking would be directly related to the overall amount of coupled running.

The purpose of Experiment 2 was to evaluate the overrunning and underdrinking effects in light of these alternative explanations. This objective was accomplished by exposing rats to FT schedules that delivered water at approximately the same local rate at which the animals earned it in Experiment 1 but independent of any wheel running requirement. Hence, the FT schedules effectively removed the motivation for coupled running and allowed the animals to express the motivation for un-

Table 3
Mean Measures of Precontingency Paired-Baseline Responding for Individual Subjects in Experiment 2

Rat	Wheel	Wheel SE	Drink	Drink SE	O_i/O_c	Dbst	Dbst SE
21	791.3	29.5	273.9	6.7	2.89	12.99	1.4
22	771.1	35.9	292.7	9.1	2.63	16.18	1.1
23	335.0	25.1	256.0	10.1	1.31	8.75	0.5
24	195.4	16.8	273.3	5.0	0.71	10.38	0.8
26	444.4	35.5	324.1	13.5	1.37	16.98	0.5
27	971.7	49.7	254.3	9.8	3.61	13.15	0.5

Note. Running and drinking measures are reported as means of total session responses. Means were based upon the last 12 sessions of the precontingency paired-baseline. Wheel = total wheel turns; Wheel SE = standard error for total wheel turns; Drink = total drinks; Drink SE = standard error for total drinks; O_i/O_c = baseline ratio of total wheel turns (O_i) to total drinks (O_c); Dbst = mean number of drinks per burst; Dbst SE = standard error for number of drinks per burst.

coupled running at any point in the session. As in Experiment 1, all schedule conditions were potentially nondepriving at the molar level. Drink burst opportunities were manipulated between 10% to 150% of the baseline average number of drinks per burst, and a tone signaled each opportunity to drink.

If the overrunning effect was caused by nonspecific motivational factors produced by intermittent reward, then the relative increase in running under the FT schedules should be approximately the same as the relative increase in Experiment 1. According to this schedule-induced account of the data, it does not matter whether the schedule is contingent or noncontingent (see Falk, 1971; Roper, 1980, 1981; Staddon, 1977)—it is necessary only that rewards be delivered on an intermittent basis.

Regarding drinking, if local disruptions of the baseline temporal distribution of drinking reduce the total effective instigation for drinking, then the overall amount of drinking should decrease because the FT schedules perturb the baseline temporal distribution to approximately the same degree as in Experiment 1. However, if the underdrinking effect results from competition with wheel running during the later portion of the session, then the magnitude of the underdrinking effect should be less in the current experiment, provided that the total amount of wheel running is reduced in the current experiment. Finally, if the reduction in drinking was caused by coupled running substituting for drinking, then the overall amount of drinking should approximate baseline because coupled running is eliminated in the current experiment.

Method

Subjects and apparatus. Six female rats served as subjects. The subjects were housed and maintained in the same manner as in Experiment 1. The apparatus was the same as Experiment 1.

Procedure. The procedure paralleled that used in Experiment 1, except there was no response contingency. The subjects received the same initial deprivation experience 1 week prior to the onset of the experiment proper, followed by the same four phases as Experiment 1. *Phase 1:* precontingency paired-baseline procedure for 68 sessions; *Phase 2:* single-baseline procedure for running and drinking for 8 sessions each; *Phase 3:* a series of four schedule constraints that allowed 10%–150% of the paired-baseline average number of drinks per burst via FT schedules for 12 sessions; and *Phase 4:* postcontingency paired-baseline procedure for 25 sessions.

The interwater intervals for the FT schedules were selected so as to approximate the local density of water that occurred in Experiment 1.

These intervals were determined by (a) calculating the average interwater interval for individual subjects in Experiment 1 and then (b) matching the current subjects with subjects in Experiment 1 on the basis of the following precontingency paired-baseline measures: total wheel turns, total drinks, the baseline ratio of running to drinking, and the average number of drinks per burst. Tables 3 and 4 show the precontingency baseline measures and FT schedule parameters for individual subjects in Experiment 2. All other procedural details in this phase of the experiment were identical to those used in Experiment 1.

Results

Running. Figure 5 shows the mean session total wheel turns. In contrast to the marked increase in total wheel turns in Experiment 1, the current constraint did not produce an increase in total wheel turns relative to paired-baseline. $F(5, 25) = 0.30, p > .91$. Total wheel turns in the single-baseline condition were not significantly different from the paired-baseline condition.

Figure 6 shows the mean wheel turns in each 10-min bin for baselines (Panel A) and total wheel turns in each 10-min bin for all schedule conditions (Panel B). Note that in terms of coupled and uncoupled running, all wheel turns were uncoupled in that they were not required to gain access to water. In the paired-baseline condition, wheel running varied significantly within the session, $F(5, 25) = 5.25, p < .05$. Post hoc analysis

Table 4
Schedule Parameters for Individual Subjects in Experiment 2

Rat	Schedules (IWI/drinks)			
	BL 1.50	BL 1.00	BL 0.25	BL 0.10
21	190.95/19.49	127.26/12.99	31.84/3.25	12.74/1.30
22	216.38/24.27	144.26/16.18	36.12/4.05	14.44/1.62
23	95.63/13.13	63.73/ 8.75	15.95/2.19	7.28/1.00
24	61.46/15.57	40.98/10.38	10.26/2.60	4.12/1.04
26	118.99/25.47	79.34/16.98	19.85/4.25	7.94/1.70
27	201.57/19.73	134.34/13.15	33.61/3.29	13.38/1.31

Note. Schedule parameters are reported as the time, in seconds, between successive drink burst opportunities (i.e., the interwater interval) and the number of drinks available per opportunity. BL = burst length ratio; IWI = interwater interval, in seconds.
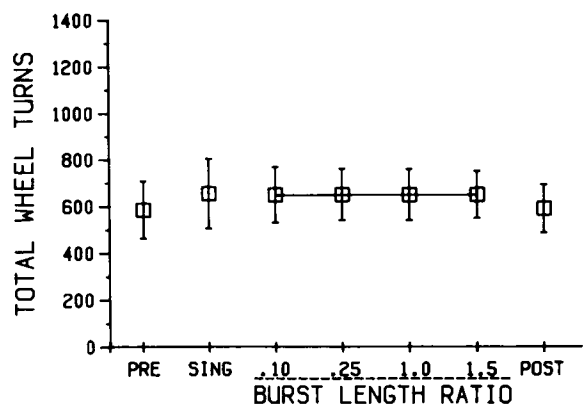
Figure 5. Mean session total wheel turns for Experiment 2. (Vertical bars represent the standard error of the means. PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline.)

indicated that running in the first 10-min bin was significantly less than in the last five 10-min bins. The local amount of running in the single-baseline condition did not vary significantly within the session, $F(5, 25) = 1.55, p > .21$. Wheel turns in the first 10-min bin in the single-baseline condition were significantly greater than in the paired-baseline condition, $t(5) = -7.14, p < .05$. This increase in running during the first 10-min bin in the single-baseline condition was also seen in Experiment 1, and again it suggests that the competition from drinking suppressed running in paired-baseline during only the first 10 min of the session.

The local amount of running in each 10-min bin under the four schedule conditions did not vary significantly as a function of the drink-burst constraint (Panel B), all $Fs(3, 15), ps > .07$. Thus, the means in each 10-min bin for the four schedule conditions were collapsed for comparisons between the local amount of running in paired-baseline and schedule conditions.

A two-factor within-subject ANOVA was used to analyze paired-baseline running with the collapsed means for uncoupled running under the four schedule conditions. The analysis indicated no significant main effect of condition (baseline vs. schedule), but there was a significant main effect of bin, $F(5, 25) = 4.56, p < .05$, and a significant interaction effect, $F(5, 25) = 4.47, p < .05$. Uncoupled running was significantly greater than baseline running in only the last 10-min bin, $F(1, 5) = 6.88, p < .05$, all other $Fs(1, 5), ps > .11$. As in Experiment 1, there was no significant difference between total paired-baseline running and total uncoupled running under the four schedule conditions, $F(1, 5) = 1.18, p > .32$.

Drinking. Figure 7 shows mean session drink totals in 0.05-ml units. As in Experiment 1, constraint on the baseline average number of drinks per burst produced a decrease in total drinks, $F(5, 25) = 8.61, p < .01$. Post hoc analysis indicated that total drinks in each schedule condition were not significantly different from each other but were significantly less than either the single- or paired-baseline drink totals. Total drinks in the single- or paired-baseline conditions were not significantly different from each other.

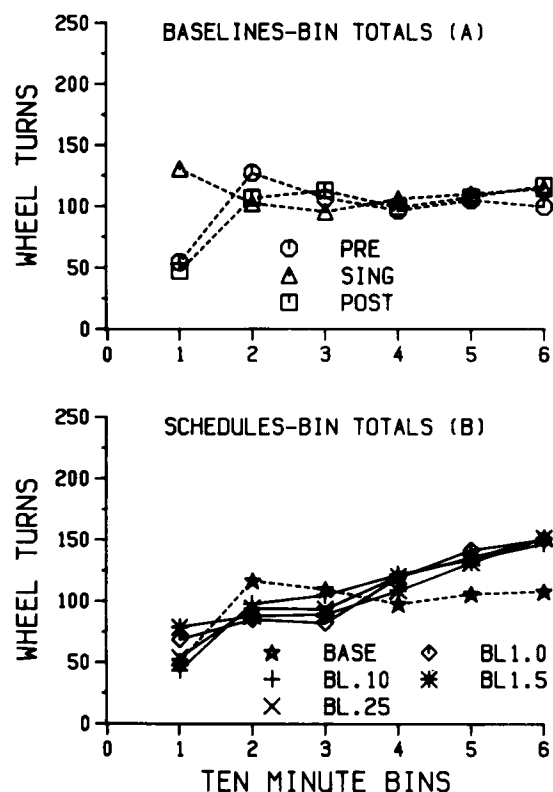Figure 8 shows mean drinks in each 10-min bin for baselines

Figure 6. Mean wheel turns in each 10-min bin in single- and paired-baselines (A) and wheel turns in each 10-min bin for all schedule conditions (B) in Experiment 2. (PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline; BL = burst length ratio; BASE = combined paired-baseline average.)

and all schedule conditions. Total drinks in each 10-min bin did not vary significantly as a function of the constraint (Panel A), all $Fs(3, 15), ps > .08$. Thus, drinks in each 10-min bin
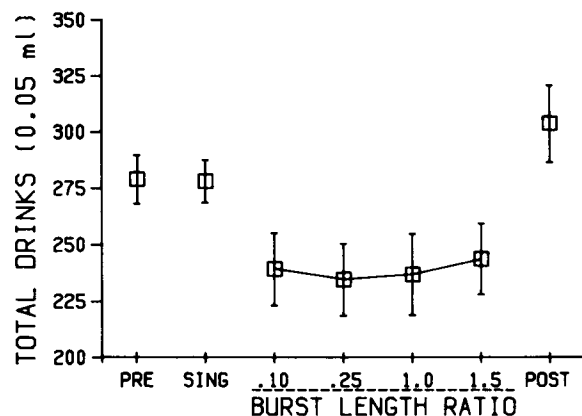

Figure 7. Mean session total drinks in 0.05-milliliter units for Experiment 2. (Vertical bars represent the standard error of the means. PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline.)
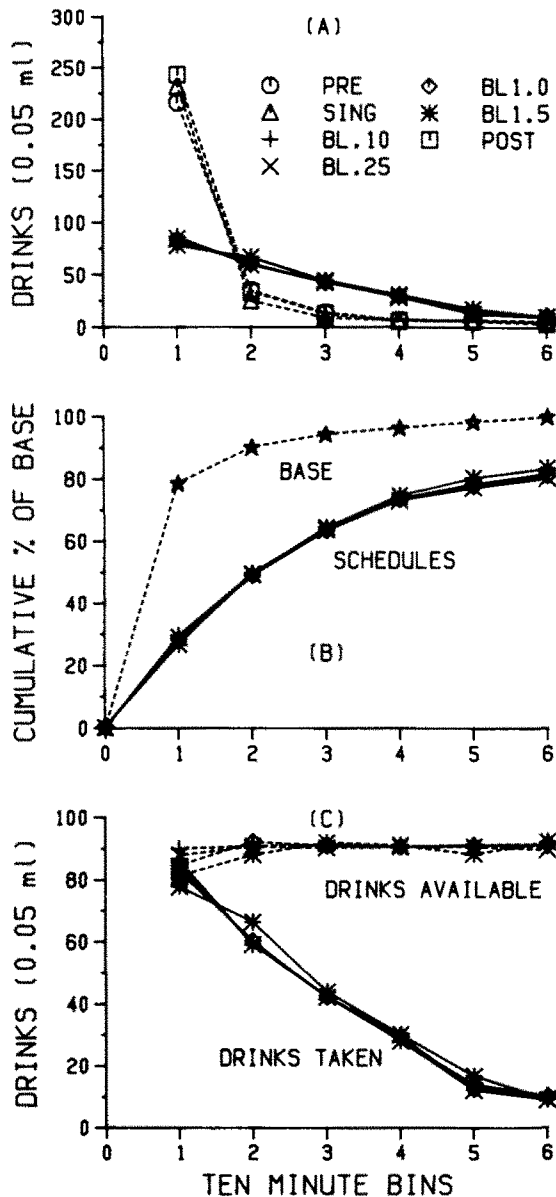
Figure 8. Mean drinks in 0.05-milliliter units in each 10-min bin (A), cumulative percent of total paired-baseline drinks (B), and drinks available versus drinks taken for all schedule conditions in Experiment 2. (PRE = precontingency paired-baseline; POST = postcontingency paired-baseline; SING = single-baseline; BL = burst length ratio; BASE = combined paired-baseline average.)

were collapsed across the four schedules for comparisons with paired-baseline. In the first 10-min bin, schedule drinks were less than paired-baseline (Panel A), $t(5) = 6.49$, $p < .01$, but exceeded baseline drinks in Bins 2, 3, and 4, all $ts(5)$, $ps < .05$. As in Experiment 1, this "excess" drinking during the later part of the session was never of sufficient quantity to maintain paired-baseline drinking, which can be seen in the cumulative percent of total baseline drinks in Figure 8B.

Figure 8 also shows the mean number of drinks available versus the number of drinks taken (Panel C). As in Experiment 1,

subjects consumed nearly 100% of the available water in the first 10-min bin. However, during the later part of the session, the rats again failed to take enough drinks to maintain total baseline water intake.

Discussion

Although constraints on the baseline drink-burst structure in the current experiment were the same as the constraints in Experiment 1, the total amount of running in the two experiments was dramatically different. Total wheel turns in each of the four schedule conditions under the current FT schedules approximated baseline, whereas the run-to-drink schedule used in Experiment 1 produced a marked increase in total running relative to baseline.

The schedule-induction explanation for the overrunning effect in Experiment 1 was not supported by the current results. Although intermittent water schedules were used in both experiments, total running in the current experiment did not exceed the baseline amount of running (cf. Levitsky & Collier, 1968).

Examination of individual subjects' wheel running data in the current experiment showed that uncoupled running approximated baseline for 5 of the 6 subjects. One subject exceeded its baseline total amount of running by approximately 65%. However, the excess running for this 1 subject was not consistent with a schedule-induced hypothesis because the largest proportion of running occurred *after* it had essentially stopped drinking. According to most accounts of schedule-induced activity (e.g., Falk, 1971, 1983; Roper, 1980, 1981; Staddon, 1977), adjunctive behavior occurs between intermittent consumption of a particular commodity, not at a point in the session when the animal is essentially satiated. Finally, contrary to the typical slow development of schedule-induced behaviors, the overrunning effect in Experiment 1 occurred on the very first day of the constraint (data not shown).

Although the current data did not support a schedule-induction explanation, one might argue that repeated pairings of the tone with water established the tone as a conditioned reinforcer in Experiment 1 and that the repeated presentation of the stimulus during the later portion of the session maintained running (Fantino, 1977; Gollub, 1977). In Experiment 2, the tone would not function as a conditioned reinforcer for wheel running because of the response-independent FT schedules, and, thus, running would not be maintained during the later part of the session.

However, from a conditioned reinforcement perspective, it is difficult to understand why the animals did not consume enough of the primary reinforcer (water) in Experiment 1 to maintain baseline water intake even though the conditioned reinforcer repeatedly signaled its availability. Furthermore, because the reinforcing effect should have been negated by satiation or extinction during the last half of the session, it is difficult to explain why the rats in Experiment 1 continued to run during this period. Finally, we have replicated the overrunning effect in our laboratory under similar fixed-ratio schedules in which the tone was absent during the last half of the session (Gawley, 1986).

Regarding drinking, the hypothesis that the underdrinking effect was caused by competition with running during the last

half of the session was not supported by the current results. The reduction in total water intake in Experiment 2 was approximately the same as in Experiment 1 despite the absence of the contingency between running and drinking. The data also did not support the hypothesis that the underdrinking effect in either of these experiments was caused by a substitution effect. If coupled running somehow used up a portion of the total instigation for drinking, then there should have been a substantial difference between the overall amount of drinking in these two experiments. However, the reduction in total drinking in both experiments was approximately the same (17%–18%).

General Discussion

Overrunning Effect

The data supported the hypothesis that coupled running does not reduce the instigation for uncoupled running. In Experiment 1 drinking was contingent on running, and the overall amount of schedule running was substantially greater than the baseline amount of running. If coupled running reduced the overall instigation for running, then the total amount of uncoupled running should have approximated the difference between the total amount of coupled running and baseline running. Instead, the amount of uncoupled running approximated total baseline running. In Experiment 2 drinking was not contingent on running, and the overall amount of uncoupled running was virtually identical to baseline for 5 of the 6 subjects. In effect, behavioral control mechanisms did not appear to subtract coupled running under nondepriving schedules from the total amount of baseline running.

It appears that deviations from the baseline temporal distribution of running accumulate over at least a 1-hr period. In both experiments the local amount of uncoupled running during the later portion of the session exceeded the local baseline amount of running. In Experiment 1, this "excess" local running appears to have been motivated by deprivation from baseline running that accumulated over the first half of the session when the rats were primarily engaged in coupled running. In Experiment 2, several rats showed local increases over baseline running during the last half of the session following decreases in the first half of the session, when most rats tended to wait by the water source rather than run in the wheel.

Previous reports of "wheel running deprivation effects" also support the notion that rats accumulate deviations when deprived of the opportunity to run. Premack (1962) showed that rats increased total running time when access to the wheel was restricted to an hour per day. Skinner (1938, p. 364) showed that as the opportunity to run in a wheel was gradually decreased over a 24-hr period, the rate of running during the remainder of the period increased. Finally, Sinclair, Gustafsson, and Aalto (1984) found that a moderately acute dose of ethanol produces hypoactivity in the running wheel, followed by a rebound effect in the running wheel the day after treatment.

The current data showed similar "rebound effects" in wheel running during the last half of the session, when the rats were either engaged in coupled running or simply waiting for water during the first half of the session. The unusual aspect of our data is that, procedurally speaking, the rats were never denied

access to the running wheel. But at the behavioral level, rats responded as though they had been deprived.

Underdrinking Effect

Behavior regulation models. A critical and surprising outcome of these experiment was the reduction in water intake. All of the schedules in both experiments were potentially nondepriving at the molar level, and, thus, it was expected that total baseline water intake would be maintained. Nevertheless, rats consistently failed to maintain baseline intake: The percent reduction from baseline intake was approximately 17%–18% in both experiments.

Despite previous reports of molar regulation under molecular constraints (Gawley et al., 1986; see also Timberlake, 1980, 1984), it is clear that disruption of local response characteristics can reduce the overall effective instigation for drinking. The current results indicate that deviations from the baseline temporal distribution of drinking do not accumulate perfectly over an hour's session as suggested by the temporal density hypothesis (Gawley et al., 1986). It may be that the instigation for drinking is tightly related to the baseline temporal distribution and that local disruptions of this response characteristic effectively reduce the overall instigation for drinking. Allison et al. (1986), however, reported that rats maintained baseline water intake when the opportunity to drink was the exact reverse of the baseline temporal pattern of drinking. However, these results are difficult to compare because the rats in that study also had access to food in the experimental chamber, which might have stimulated postprandial drinking.

Although it is true that the temporal density hypothesis (Gawley et al., 1986) adequately predicts the compensatory adjustments in the rate of drinking in order to reduce deviations from the baseline temporal distribution (see also Mook & Dreifuss, 1986), additional assumptions are necessary to account for why these deviations fail to accumulate over an hour session.

A physiological perspective. The failure to accumulate deviations from baseline drinking suggests the possible influence of physiological satiation mechanisms over the reduction in drinking. When water-deprived rats are allowed free access to water, the feedback signals that terminate drinking appear to arise from short-term orogastric mechanisms (Hall & Blass, 1977; Rolls & Rolls, 1982; Toates, 1980a). These short-term mechanisms effectively inhibit water intake while water is transferred from the gut into the extracellular and cellular compartments. There is evidence, however, which suggests that rehydration may be rapid enough to allow long-term satiation mechanisms to terminate drinking in rats (Corbit, 1969; Hatton & Bennett, 1970). Hatton and Bennett (1970), for example, have shown that after 23-hr water deprived rats start drinking, it takes only approximately 10 min for plasma osmolality to return to approximately ad lib levels. Moreover, the quantity of water absorbed from the gut necessary to achieve this effect appears to be relatively small (i.e., as little as 5 ml).

Although the results of the Hatton and Bennet (1970) study do not necessarily exclude short-term mechanisms in the termination of drinking (see Hall & Blass, 1977), we argue that long-term satiation mechanisms such as plasma osmolality may have exerted more control over the termination of drinking under

the intermittent schedules than they did when water was ingested in a relatively continuous and rapid manner in baseline (see also Clifton, Popplewell, & Burton, 1984, for a similar argument about reduced rate of food intake). Because a small quantity of absorbed water (5 ml) can return plasma osmolality to approximately ad lib levels after only 10 min of drinking (Hatton & Bennett, 1970), activation of this long-term mechanism may have occurred at approximately the same time from the onset of drinking under both the intermittent schedules and the baseline, but with substantially different amounts of water in the gut. Thus, total water intake was less under the intermittent schedule.

Another possibility is that the postsession watering procedure, in conjunction with the disruption of drinking, affected the rats' allocation of drinking (see Toates, 1979). For example, it may be that rats prefer to delay part of their water intake closer to feeding times in order to reduce the dehydrating (hypovolemic) effects of a meal that may be particularly aversive under water deprivation. This hypothesis, however, assumes that rats will reduce intake in anticipation of the future availability of water over at least an hour. The matter is currently under further investigation.

Implications for Behavior Regulation Models

Both molar behavior regulation models (Allison, 1976, 1980; Hanson & Timberlake, 1983; Staddon, 1979; Timberlake, 1980) and more molecular behavior regulation models (Gawley et al., 1986; see also Timberlake, 1984) have generally assumed that different behaviors are governed by rather simple regulatory processes. The current data suggest that aspects of the motivational structure of running and drinking are different and that both behaviors are controlled by rather complex regulatory mechanisms.

One major difference between these two motivational systems is that drinking is heavily influenced by, though not exclusively controlled by, the internal body-fluid state of the animal (see Toates, 1979, 1980b). Hence, it would be expected that similar fluids (e.g., water and saccharin solution) that were linked by a contingency schedule would be highly substitutable because both fluids would be equally effective in reducing thirst (see Allison & Moore, 1985, Experiment 2). Conversely, running does not seem to have a complex internal control system, and, according to our data, different types of running may not be substitutable.

It also appears that the effect of short-term deprivation is different for drinking than it is for running. Although deviations from the baseline temporal distribution of drinking evoke immediate compensatory adjustments in the local rate of drinking (Gawley et al., 1986), the deviations dissipate within an hour probably because of the change in the effective set-point (Corbit, 1969; Hatton & Bennett, 1970). On the other hand, accumulated deviations from baseline running do not appear to dissipate over the same hour period.

At a procedural level, molar behavior regulation models typically assess long-term set-points under free-access baselines. However, this baseline procedure does not appear to be a pure measure of a long-term set-point for drinking. In fact, depending on its length, drinking in baseline is probably controlled by both long-term and short-term mechanisms (Hall & Blass, 1977). Hence, baseline assessment of only molar response characteristics may require distributing limited access periods across the session in order to avoid contamination by short-term mechanisms (see Allison & Moore, 1985; Timberlake, 1979; and Roper, 1981, for baseline procedures that may control for these short-term/long-term interactions). In general, we need a model of baseline behaviors that includes both short- and long-term regulatory processes in order to predict more accurately the compensatory adjustments in responding under schedule constraint.

It is also clear that the type of schedule that one uses to assess regulatory processes is quite important. For example, Gawley et al. (1986) reported that under nondepriving reciprocal schedules the instigation for wheel running was higher during the later portion of the contingency session than at the beginning of the session. However, because of the reciprocal contingency, the rats actually had to drink in order to run during the later portion of the session. Thus, the reciprocal schedules required that any excess running be contingent on a proportionate amount of excess drinking—a relation that apparently suppressed overrunning during the later part of the session.

But, as shown in the current experiment, when the motivational systems for drinking and running could be expressed independently, rats not only continued to run during the later portion of the session but also failed to maintain baseline total water intake. Hence, generalizations about whether animals maintain baseline levels of responding under nondepriving schedules need to be qualified by (a) the use of reciprocal or nonreciprocal schedules and by (b) consideration of how physiological processes might impose restrictions on responding.

Although general-purpose regulation models were an important first step, the current results suggest that it is time to focus more on the system-specific characteristics of motivational processes. That is, from a behavior regulation perspective, we should not assume that all motivational systems are governed by regulatory processes with identical system characteristics or that regulation is always organized around daily response totals. Our results indicate that general-process behavior regulation models are limited in their accuracy and their time course of prediction and that more dynamic, system-specific regulation models need to be developed.

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