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TECHNIQUES FOR ESTABLISHING SCHEDULES WITH WHEEL RUNNING AS REINFORCEMENT IN RATS

IVER H. IVERSEN

UNIVERSITY OF NORTH FLORIDA

In three experiments, access to wheel running was contingent on lever pressing. In each experiment, the duration of access to running was reduced gradually to 4, 5, or 6 s, and the schedule parameters were expanded gradually. The sessions lasted 2 hr. In Experiment 1, a fixed-ratio 20 schedule controlled a typical break-and-run pattern of lever pressing that was maintained throughout the session for 3 rats. In Experiment 2, a fixed-interval schedule of 6 min maintained lever pressing throughout the session for 3 rats, and for 1 rat, the rate of lever pressing was positively accelerated between reinforcements. In Experiment 3, a variable-ratio schedule of 20 or 35 was in effect and maintained lever pressing at a very stable pace throughout the session for 2 of 3 rats; for 1 rat, lever pressing was maintained at an irregular rate. When the session duration was extended to successive 24-hr periods, with food and water accessible in Experiment 3, lever pressing settled into a periodic pattern occurring at a high rate at approximately the same time each day. In each experiment, the rats that developed the highest local rates of running during wheel access also maintained the most stable and highest rates of lever pressing.

Key words: wheel-running reinforcement, fixed-ratio schedules, fixed-interval schedules, variable-ratio schedules, reinforcer duration, extinction, circadian rhythms, lever pressing, rats

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The present research sought to establish methods that might enable stable schedule-controlled emission of operant behavior over several hours without the use of food or water deprivation. Such methods would extend the domain of application of operant conditioning. Of course, food and water reinforcers have been implemented successfully in operant conditioning research and application. Electrical brain stimulation has also been used to establish schedule control of operant behavior (e.g., Pliskoff, Wright, & Hawkins, 1965). These customary reinforcers require manipulation of the subject's environment in terms of deprivation regimens or surgery. Reinforcers free of such requirements have been established, for example, by using access to a running wheel as the reinforcer. Several studies have demonstrated, with rats as subjects, that access to wheel running can reinforce other behavior such as eating, licking, or lever pressing (e.g., Collier & Hirsch, 1971; Kagan & Berkun, 1954; Pierce, Epling, & Boer, 1986; Premack, 1962, 1965; Premack, Schaeffer, & Hundt, 1964; Timberlake & Allison, 1974; Timberlake & Wozny, 1979).

Wheel-running reinforcement therefore seems to be a candidate for the present purpose because no special deprivation or home-cage arrangement is required. Wheel-running reinforcement has often been used as a method to study theoretical issues regarding behavior regulation and reinforcement processes (e.g., Mazur, 1975; Tierney, Smith, & Gannon, 1983; Timberlake & Wozny, 1979). However, wheel-running reinforcement has not been used extensively as a technique to study the effects of other independent variables on operant behavior.

The purpose of the present research was to explore some techniques that might enable wheel running to be used as an effective reinforcer to obtain stable operant behavior in schedule-appropriate patterns over long sessions. These methods can be used to establish a baseline of operant behavior against which the effects of numerous variables can be assessed. Given that no food or water deprivation is required, schedule control using wheel-running reinforcement would be ideal for studies involving drugs or toxins that are likely to affect consummatory and digestive processes that in turn affect the efficacy of food or water reinforcers used to study the effects of the drugs on the operant behavior per se. The present research was exploratory and was not undertaken to answer theoretical questions or to provide systematic parametric manipulations of schedule variables.

Previous methods using wheel-running re-

Reprint requests should be sent to Iver Iversen, Department of Psychology, University of North Florida, Jacksonville, Florida 32216.

inforcement have commonly involved either relatively short sessions in the 10- to 30-min range (e.g., Premack et al., 1964) or relatively long (e.g., 20 to 60 s) or unspecified durations of access to running (e.g., Collier & Hirsch, 1971; Pierce et al., 1986). More critically, the reported increases in operant behavior by access to wheel running often have been modest; in general, the increase has been by a factor of two to six compared to a baseline with either free access to running or no access to running (e.g., Kagan & Berkun, 1954; Mazur, 1975; Premack et al., 1964). An additional methodological consideration is that when eating or licking is used as the operant response with contingent wheel running, the increases in operant responding are often masked by the fact that the operant response and the contingent wheel-running activity compete for time. That is, the time spent running is reduced compared to free access, when running is made contingent on the operant response, and more time becomes available for the operant response. Therefore, part of the increase attributed to the reinforcement effect may stem from this change in time allocation to running (see Dunham, 1977; Timberlake & Wozny, 1979).

Thus, lever pressing may be more suitable than either eating or licking as the operant response when long sessions and schedule-controlled performance are at issue, because unreinforced lever pressing commonly is absent or occurs at a low rate of a few presses per hour. A survey of the literature revealed few studies in which lever pressing was the operant response with wheel-running reinforcement. In one study, Collier and Hirsch (1971) established control over operant lever pressing by access to wheel running under fixed-ratio (FR) schedules ranging from FR 1 to FR 80. For each reinforcer, wheel running was accessible for as long as the rats kept running; when the rats stopped for 15 s, the brake was activated to prevent further running, the FR schedule had to be engaged for the next reinforcer, and so on. Collier and Hirsch used 2-hr sessions, and lever pressing occurred at frequencies up to about 500 per session (roughly four lever presses per minute) under FR 80. Collier and Hirsch did not report how lever pressing was distributed over time within sessions.

The present study attempted to make certain technical modifications that might enable higher lever-pressing rates (than in Collier & Hirsch, 1971) and stable maintenance of lever pressing throughout long sessions. Premack et al. (1964) were able to maintain operant licking with short (2- to 4-s) periods of access to running. By limiting the access to running (the reinforcer duration) to the typical temporal characteristics of food and water reinforcers (in the 4- to 6-s range), more opportunities for reinforcement are generated than with relatively long or unlimited access to wheel running. The present experiments used these short reinforcer durations to attempt to make the rates of lever pressing exceed those reported in earlier studies. Furthermore, in the present experiments, reinforcer durations were reduced gradually, and schedule parameters were incremented stepwise to prevent possible deterioration or breakdown of established performance that may occur with sudden large changes in schedule values. The present experiments attempted to establish operant lever pressing under FR, fixed-interval (FI), and variable-ratio (VR) schedules using wheel running as reinforcement.

Technically, with wheel-running reinforcement, the subject is deprived of wheel running before the session because a running wheel customarily is not available in the home cage. However, deprivation of wheel running apparently has not been explored as an independent variable in previous work. To determine whether deprivation of wheel running is necessary for the maintenance of operant behavior with wheel-running reinforcement, Experiment 3 maintained the reinforcement schedules continuously in successive 24-hr sessions with food and water available in the apparatus. Experiment 3 therefore sought to examine the feasibility of using wheel-running reinforcement in the study of circadian rhythms of operant behavior.

GENERAL METHOD

Subjects

In all experiments the subjects were female Long-Evans rats, 3 to 4 months old at the start of each experiment. The rats were neither food nor water deprived and had free access to both food and water in individual Wahmann home cages (17.6 cm wide, 24 cm deep, and 18 cm high). A 12:12 hr light/dark cycle operated in the colony room. In the last condition of Experiment 3, food and water were available in the experimental chamber.

Apparatus

The running wheel was 15.5 cm wide, with a circumference of 103.7 cm. The running surface consisted of 2-mm steel bars spaced every 8.5 mm. The wheel could turn in either direction. Rotation of the wheel was recorded as one of three magnets mounted equidistant on the circumference of the wheel passed a reed relay mounted on the support of the wheel. This method did not differentiate the direction of wheel rotation. A modified relay served as a remotely controlled rim brake. The brake released the wheel instantly; at a speed of one revolution per second the wheel would come to a stop in about 0.5 s. The wheel was suspended on one side. The other side was a stationary wall with a lever (2 cm by 2 cm) placed to the left of the midline of the wall and 5 cm above the running surface. A lever press was recorded as a 3-mm depression of the lever with a force greater than 0.1 N. A food cup (3 cm by 2 cm by 1 cm) was mounted 5 cm to the right of the lever. Noyes 45-mg food pellets were delivered into this cup in the last condition of Experiment 3. An aperture was located between and 2 cm above the level of the lever and the food cup; a water spout was presented in this aperture in the last condition of Experiment 3.

The running wheel apparatus was enclosed in a sound-attenuating cubicle with a fan and masking noise. Sessions were conducted in darkness.

Procedure

All experiments followed the same general procedure. Initially, access to running was free throughout the session (one to six sessions). Next, access to running was restricted to gradually shorter time periods to ensure that running was under control of the reinforcer operation (two to five sessions). Finally, access to running was made contingent upon lever pressing, which was then maintained under different schedule conditions in each experiment.

In Experiments 1 and 2 and the first part of Experiment 3, sessions lasted approximately 2 hr and were scheduled at about the same time of the day for each subject. Sessions were scheduled between 9 a.m. and 4 p.m., and each subject had two or three sessions each week. In the last condition of Experiment 3, the rats remained in the apparatus for consecutive days, with the reinforcement schedules operating continuously and with food and water available.

Reinforcer control. The second condition of gradually restricting access to running is similar to what is commonly called magazine training with food or water reinforcers. Reinforcer control is described here because the method used was common for all experiments.

In general, after sessions with free access to running, the brake was first locked in 5-min periods separated by 1-min periods with free access to running. The access period was then reduced to 30 s, to 15 s, and in some cases to 10 or 9 s. Reinforcer control was considered established when running occurred in all access periods and within 1 or 2 s after release of the brake.

In Experiment 1, a 2000-Hz tone sounded for as long as running in the wheel was possible (i.e., for as long as the brake was released from the wheel). In Experiments 2 and 3, the tone was omitted. Without the tone, the distinct sound from the relay that controlled the brake proved to be sufficient to control prompt onset of running when the brake was released.

For all rats, lever pressing occurred sporadically (at a rate of approximately five lever presses per hour) during sessions with free access to running or reinforcer control. In the first session in which access to running was made contingent on lever pressing, the low frequency of lever pressing was sufficient to bring the subject in contact with the contingency; therefore, shaping of lever pressing was not necessary for any rat.

EXPERIMENT 1

The purpose of Experiment 1 was to replicate and expand upon previous work that had established lever pressing under an FR schedule of wheel-running reinforcement. A fixed number of lever presses produced brief access to running in the wheel. In a survey of the comparative effects of different reinforcers, Hogan and Roper (1978) indicated that extinction of operant behavior previously maintained with wheel-running reinforcement had not been documented. Therefore, extinction of

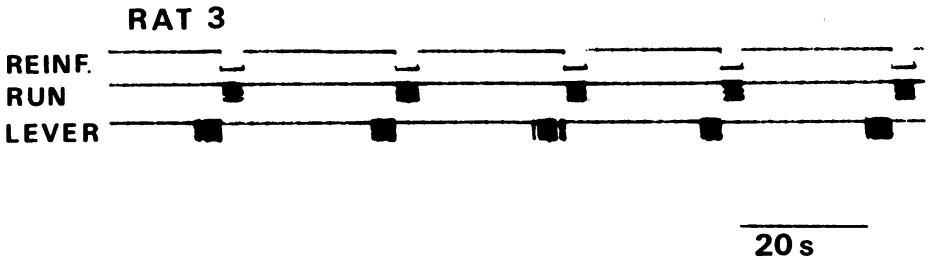

Fig. 1. Segment of an event record showing reinforcement (access to wheel running), wheel running, and lever pressing. Lever pressing was maintained under FR 20 with 4-s access to wheel running as reinforcement. The pen for reinforcement was deflected for as long as the brake to the wheel was released. The pen for running was deflected for each third of a revolution of the wheel. The pen for lever pressing was deflected for each lever press.

lever pressing was studied in Experiment 1 by abolishing access to running in two sessions.

Method

Procedure

Four rats were used. After three sessions of free access to running, access was restricted gradually to 15-s periods during three sessions. A 2000-Hz tone sounded during access. Rats 1, 2, and 3 were exposed to the same sequence of FR schedules. FR 1 was in effect for two sessions and FR 2 for two sessions. The FR size was incremented by a unit of one each session to FR 10 (eight sessions). Then FR 10 was maintained for five sessions. Next, the FR was further increased by two for each of five sessions up to FR 20. The FR 20 was maintained for the rest of the experiment.

After 14 sessions under FR 20, the reinforcer duration was reduced from 15 to 7 s for four sessions. The reinforcer duration was reduced further to 4 s for eight sessions. Finally, two extinction sessions were scheduled, with no access to running. These sessions were terminated after 20 min without lever pressing.

For Rat D lever pressing was not maintained well, and this rat was removed from the experiment. Some attempts were made to increase the lever-pressing output. The procedures and some results for Rat D are described at the end of the Results section.

Results

All rats (including Rat D) acquired lever pressing as operant behavior under the FR schedule of wheel-running reinforcement. To illustrate the general performance pattern, Figure 1 presents a sample event record showing reinforcement (access to the wheel), wheel running, and lever pressing from the last condition of FR 20 with a 4-s reinforcer duration for Rat 3. Lever pressing occurred in a burst before reinforcer delivery, and wheel running began promptly with access to running. Pauses in lever pressing followed reinforcements.

Figure 2 shows the rate of lever pressing for each session under FR reinforcement for Rats 1, 2, and 3. (The time base for the rate calculation was the session duration minus the cumulated reinforcer time.) The rate of lever pressing increased gradually as the FR size was increased from 1 to 10. When the schedule size was increased to FR 20, the lever-pressing rate increased further. With the 15-s reinforcer duration, the FR 20 reliably sustained a lever-pressing rate of 20 to 30 responses per minute for Rat 1, two to seven responses per minute for Rat 2, and 10 to 19 responses per minute for Rat 3. When the reinforcer duration was decreased to 7 s and then to 4 s, lever pressing was maintained for all rats, with a further increase in lever-pressing rate for Rat 3.

Figure 3 shows sample cumulative records of lever pressing under FR 20 with the 15-s reinforcer duration. The pattern of responding was a burst of lever pressing preceding each reinforcement and a pause in responding after reinforcement. For Rats 1 and 3, this break-and-run pattern was maintained at a very reliable pace throughout the session. For Rat 2, performance was characterized by occasional very long pauses.

Figure 4 provides cumulative records of lever pressing from the first extinction session; the wheel was locked throughout these sessions. For all rats, lever pressing occurred in long

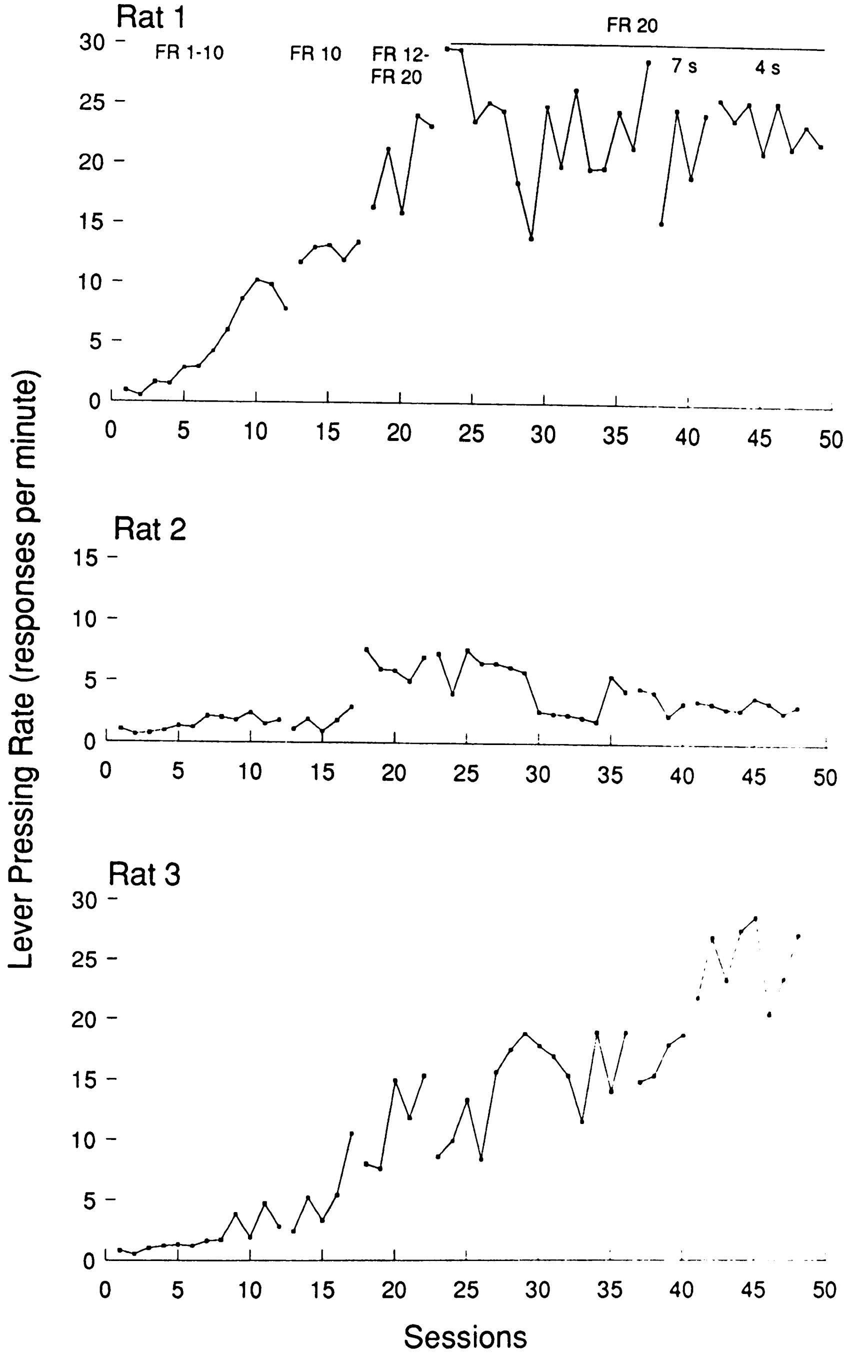

Fig. 2. Rate of lever pressing for each session in Experiment 1. Lever pressing was maintained under an FR schedule with access to wheel running as reinforcement. Changes in FR size are indicated; reinforcer duration was 15 s except for the last two conditions under FR 20, in which reinforcer duration was 7 s and 4 s.

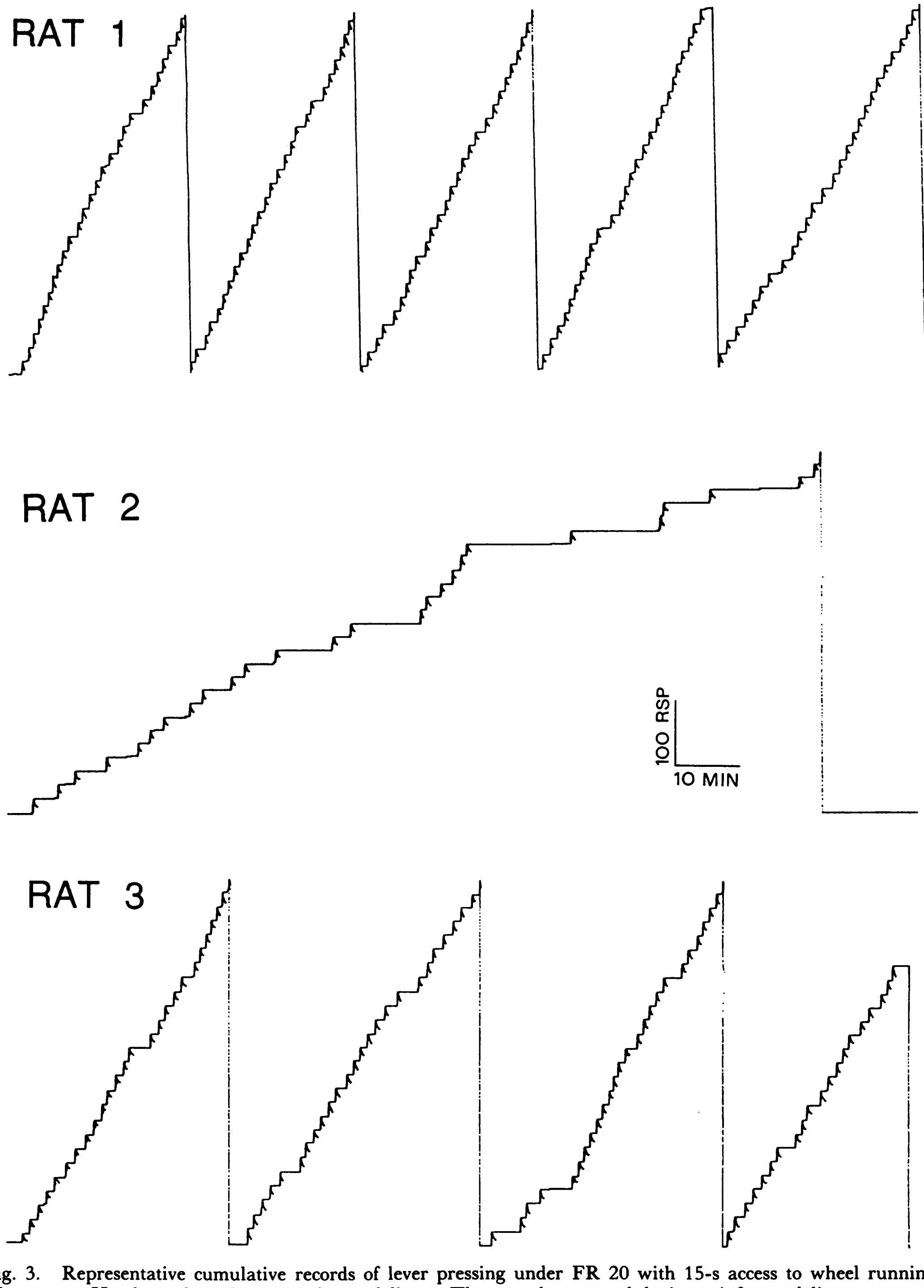

Fig. 3. Representative cumulative records of lever pressing under FR 20 with 15-s access to wheel running as reinforcement. Hatch marks indicate reinforcer delivery. The recorder stopped during reinforcer delivery.

bursts separated by pauses that gradually became longer as the session progressed. Several bursts of lever pressing considerably exceeded the previous requirement of 20 presses under the FR schedule. For example, the bursts ending at A, B, and C in Figure 4 were 112, 101, and 268 responses long. The session lasted 136, 76, and 128 min, with a total of 1,972, 465, and 1,693 responses emitted by Rats 1, 2, and 3, respectively. The second extinction session lasted 121, 66, and 62 min, with 688, 303, and 181 responses emitted by Rats 1, 2, and 3, respectively.

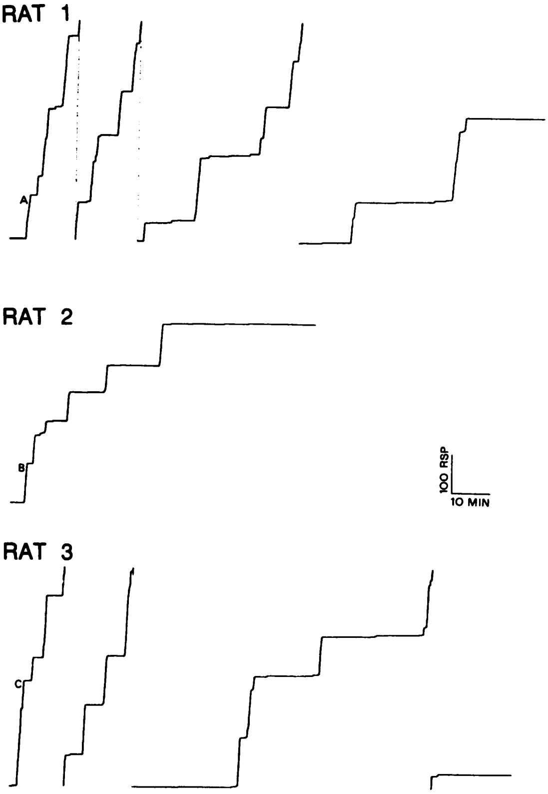

Fig. 4. Cumulative records of lever pressing in extinction after FR 20 with wheel-running reinforcement. Sessions ended after 20 min without lever pressing.

Wheel Running

Table 1 shows the overall rate of running and running speed during wheel access. Running speed was not defined under the free-access condition. The unit of wheel running was a full revolution. Data are presented for the last three sessions of each condition except for FR 1, in which only two sessions were given. For all rats, the restriction on running by requiring lever pressing to produce access to running first lowered the overall running rate (FR 1). For Rat 1, under FR 10 and FR 20, the overall running rate then increased considerably, compared to running under free access and FR 1. For example, the average overall running rate under free access was 124 revolutions per hour, whereas the average running rate under FR 10 was 405 revolutions per hour. Similarly, for Rat 3, the average overall running rate was considerably higher under FR 20 than during free access or FR 1. However, for Rat 2, the overall running rate did not reliably exceed that of free access and actually decreased during FR 10.

The running speed during reinforcement increased throughout the experiment for each rat. The highest running speed occurred when the reinforcer duration was reduced to 4 s under FR 20. Converted to distance run, on average Rats 1 and 3 ran a distance of 360 cm in a 4-s reinforcement period; for Rat 2, the distance was 244 cm in a 4-s reinforcement period.

Rat D

This rat was exposed to the same initial procedure as the other rats up to the end of FR 10 training. However, even though lever pressing did occur during each session, the rate was as low as 0.65 responses per minute over the last three sessions under FR 10. In an attempt to boost performance, wheel running was placed under free access for three sessions. The FR 10 was then scheduled for five additional sessions. However, the lever-pressing rate did not increase. The schedule was then reduced to FR 6 for 10 sessions. For the last three sessions, the lever-pressing rate was 1.2 responses per minute. Neither the exposure to free running nor the reduction in FR size dramatically improved lever-pressing performance, and the experiment was terminated at this point for Rat D.

For Rat D, the overall running rate under free access was 268 revolutions per hour (267, 134, and 403 for three sessions) for the first free-access sessions and 402 revolutions per hour (486, 505, and 217) for the three sessions scheduled after FR 10. The running speed under FR 1 was 0.30 revolutions per second

Table 1

Overall rate of wheel running (revolutions divided by session time, expressed as revolutions per hour) and speed of running during wheel access (revolutions divided by total reinforcer time, expressed as revolutions per second) in Experiment 1. Data are shown for the last three sessions of each condition; for FR 1, only two sessions were scheduled. Averages are shown, followed by absolute values in parentheses. The reinforcer duration is given in parentheses next to the FR value in each condition. Running speed is not defined under free access.

Subject	Condition	Overall running rate	Running speed
Rat 1	Free access	124 (94, 101, 177)	—
	FR 1 (15 s)	66 (57, 77)	0.23 (0.18, 0.28)
	FR 10 (15 s)	405 (468, 381, 367)	0.47 (0.56, 0.44, 0.43)
	FR 20 (15 s)	394 (434, 381, 367)	0.61 (0.63, 0.65, 0.57)
	FR 20 (4 s)	217 (187, 264, 202)	0.87 (0.80, 0.96, 0.85)
Rat 2	Free access	83 (81, 66, 101)	—
	FR 1 (15 s)	63 (52, 74)	0.22 (0.20, 0.26)
	FR 10 (15 s)	29 (21, 39, 29)	0.26 (0.24, 0.31, 0.24)
	FR 20 (15 s)	95 (117, 64, 105)	0.38 (0.40, 0.36, 0.39)
	FR 20 (4 s)	22 (30, 21, 16)	0.59 (0.70, 0.52, 0.56)
Rat 3	Free access	153 (138, 149, 172)	—
	FR 1 (15 s)	121 (133, 109)	0.29 (0.26, 0.32)
	FR 10 (15 s)	170 (235, 102, 173)	0.49 (0.62, 0.39, 0.46)
	FR 20 (15 s)	328 (367, 303, 315)	0.53 (0.56, 0.58, 0.45)
	FR 20 (4 s)	206 (204, 155, 261)	0.87 (0.92, 0.80, 0.89)

(0.27 and 0.33), under FR 10 it was 0.35 (0.33, 0.37, and 0.35), and under FR 6 it was 0.34 (0.31, 0.38, and 0.33). Thus, even though the overall running rate in free access was higher for Rat D than for any of the other rats (Table 1), the speed of running did not increase over the course of the experiment for Rat D, as it did for the other rats.

DISCUSSION

These results demonstrate that lever pressing could be acquired and maintained under an FR schedule of wheel-running reinforcement. Even when the reinforcer was a mere 4 s of access to running, the FR schedule maintained a stable pattern of responding. For Rats 1 and 3 in particular, responding was highly regular throughout the 2-hr sessions. The results confirm and extend previous findings using wheel-running reinforcement on FR schedules. Premack et al. (1964) established operant licking under FR 5 to FR 300 with 20 s of wheel-running reinforcement in 20-min sessions. In the same experiment, the reinforcer duration was manipulated under FR 10 from 2 to 20 s. As in the present experiment, the rate of operant responding was not very sensitive to the manipulation of reinforcer duration. Collier and Hirsch (1971), using food-deprived rats, also established operant lever pressing with wheel-running reinforcement under FR schedules ranging from 1 to 80. In their experiment, wheel running was available for each reinforcer for as long as the rat ran and did not pause longer than 15 s. In the Collier and Hirsch study, the total number of lever presses per 2-hr session (averaged for 6 rats) was approximately 350 for FR 20 (as judged from their Figure 1). In comparison, in the present experiment, the total number of lever presses per 2-hr session was 2,565, 380, and 2,449 for Rats 1, 2, and 3, respectively (averaged for the last three sessions under FR 20 with the 4-s reinforcer duration). In turn, the average overall number of reinforcers obtained per 2-hr session was 128, 19, and 122 for Rats 1, 2, and 3, respectively. At least for Rats 1 and 3, the FR 20 with a 4-s reinforcer duration thus enabled a considerable gain in the amount of operant behavior controlled by the reinforcement schedule, compared to an FR 20 schedule that had a free reinforcer duration (Collier & Hirsch, 1971).

Running speed increased the most for Rats 1 and 3, who exhibited the largest increases in lever-pressing rate. For Rat D, running speed did not increase, and lever pressing was poorly maintained. For Rat 2, the running speed did increase but not as much as for Rats 1 and 3, and the lever-pressing rate was not as high as for Rats 1 and 3 (but it was considerably higher than for Rat D). Taking all the data into consideration, a critical variable in the control of operant lever pressing by contingent wheel running may thus be the speed of running during reinforcer access.

EXPERIMENT 2

In Experiment 1, the FR schedule made the reinforcer rate vary with the response rate. The purpose of Experiment 2 was to determine whether lever pressing could be maintained under a schedule that holds the reinforcer rate relatively fixed. An FI schedule was arranged so that when a given time interval had elapsed, the first lever press would produce access to wheel running.

METHOD

Procedure

Three rats (Rats 4, 5, and 6) were used. After three sessions with free access to running, reinforcer control was established over three sessions by gradually restricting access to running to 9-s periods. For one session, each lever press produced 9-s access to running. Then an FI schedule was programmed. Table 2 shows the sequence of experimental conditions. First, the FI was increased in small steps each session to FI 2 min and then to FI 6 min. Under the FI 6-min schedule, the reinforcer duration was decreased in small steps from 9 to 5 s. For Rat 4, the reinforcer duration was then changed to 15 s and then back to 5 s. The total number of sessions under the FI schedule was 54, 53, and 56 for Rats 4, 5, and 6, respectively. Finally, one session of extinction was scheduled for each rat, during which lever pressing did not produce access to running; the running wheel was locked throughout this session. The extinction session lasted until lever pressing had stopped for 15 min.

Table 2

The sequence of experimental conditions for Experiment 2. Lever pressing produced access to wheel-running reinforcement under an FI schedule.

Subject	Condition	Reinforcer duration (s)	Sessions (Rats 4, 5, 6)
4, 5, 6	FI 10 s to FI 2 min	9	6, 6, 6
4, 5, 6	FI 2 min	9	8, 8, 8
4, 5, 6	FI 2 min to FI 6 min	9	6, 7, 8
4, 5, 6	FI 6 min	9	12, 20, 20
4, 5, 6	FI 6 min	9 to 5	4, 4, 4
4, 5, 6	FI 6 min	5	10, 8, 8
4	FI 6 min	15	10
4	FI 6 min	5	5
4, 5, 6	Extinction	—	1, 1, 1

RESULTS

Lever pressing was maintained reliably under the FI schedule for each rat. Figure 5 shows the overall lever-pressing rates for each session. (During free access to running, lever pressing occurred sporadically at rates of a few presses per hour.) For Rat 4, the consistently highest response rates (five to eight responses per minute) occurred under FI 6 min with the 15-s reinforcer duration. For Rats 5 and 6, the lever-pressing rates were lower than for Rat 4 but were maintained at an approximately constant level in all conditions after FI 2 min. For all rats, the overall lever-pressing rates were considerably lower than those obtained in Experiment 1 under FR schedules.

Figure 6 shows sample cumulative records of lever pressing under the FI 6-min schedule with a 9-s reinforcer duration. For Rat 4, almost all interreinforcer intervals were characterized by a positively accelerated local rate of lever pressing. For Rats 5 and 6, a positively accelerated pattern occurred only occasionally (A in Figure 6); the local lever-pressing rate was somewhat variable for Rat 5 and became fairly constant toward the end of the sessions for Rat 6. The interreinforcer intervals exceeded the scheduled FI 6-min duration on occasion for Rats 5 and 6 (B in Figure 6).

Even though the overall lever-pressing rates were relatively low compared with those obtained in Experiment 1, the FI schedule did maintain a relatively high number of lever presses per reinforcer. Averaged for the last three sessions of FI 2 min (9-s reinforcer), FI 6 min (9-s reinforcer), and FI 6 min (5-s reinforcer), the lever presses per reinforcer were 11.8, 48.6, and 39.4 for Rat 4; 5.2, 16.2, and 21.0 for Rat 5; and 4.8, 15.6, and 11.4 for Rat 6. Thus, consistently more lever pressing was sustained per reinforcer under FI 6 min than under FI 2 min. Because of the long interreinforcer intervals, the low overall response rate under the FI 6-min schedule could result in an accumulation of even more responses per

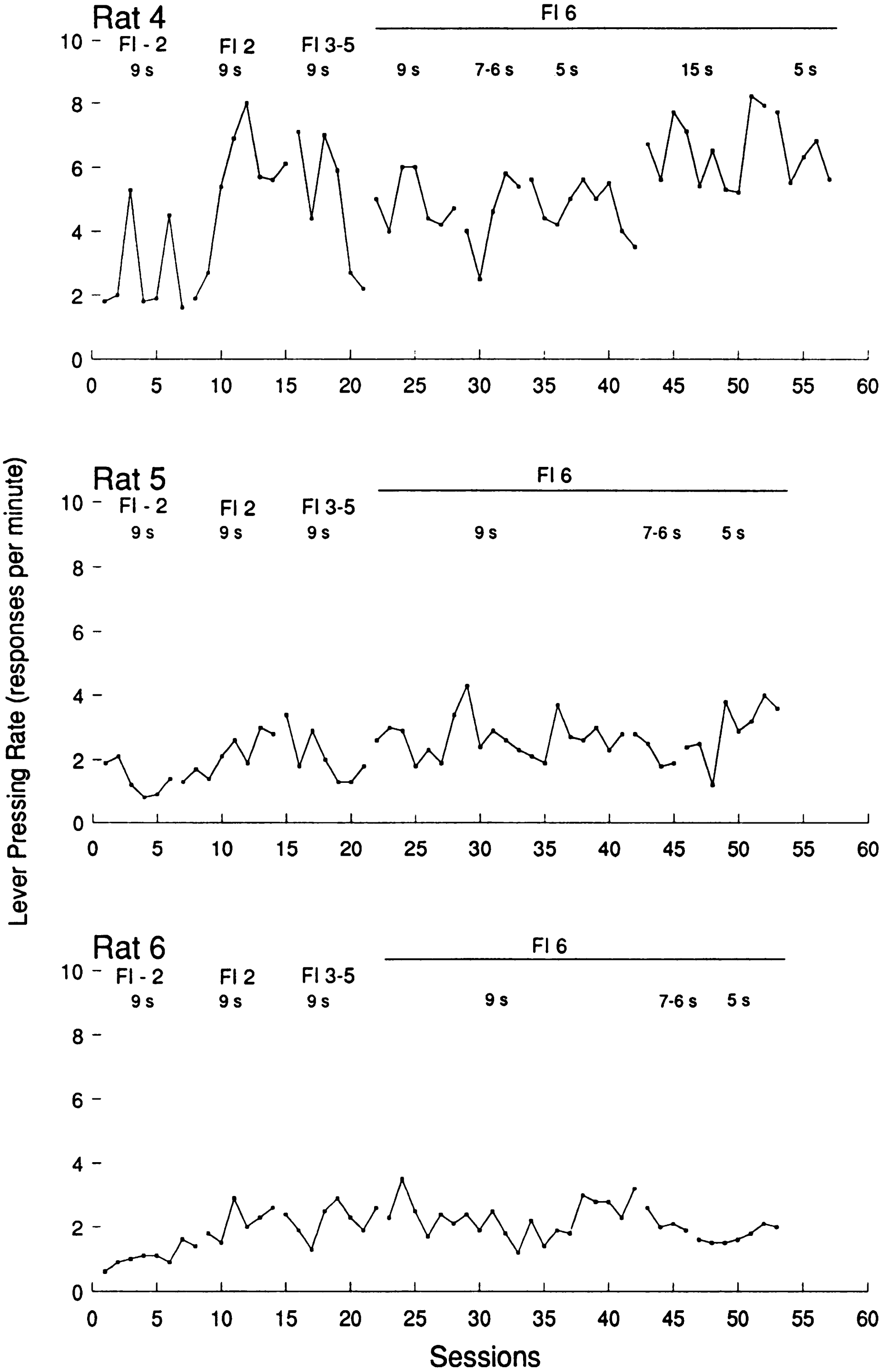

Fig. 5. Rate of lever pressing for each session in Experiment 2. Lever pressing was maintained under an FI schedule with access to wheel running as reinforcement. Changes in FI size (minutes) and reinforcer duration (seconds) are indicated. In the first condition, FI size was increased gradually from FI 10 s to FI 2 min.

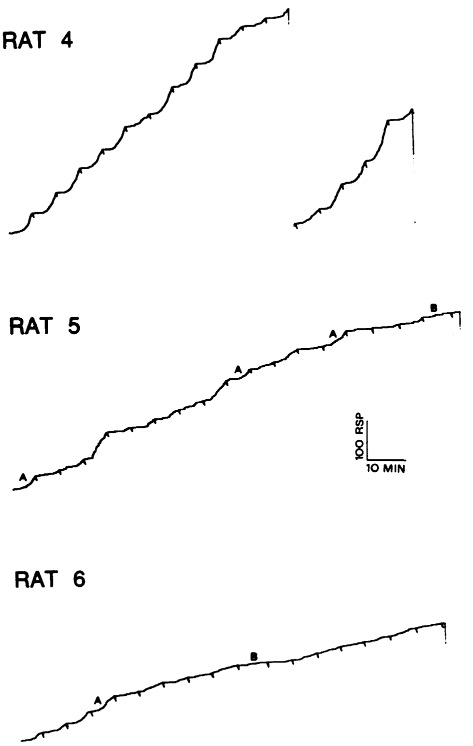

Fig. 6. Representative cumulative records of lever pressing under FI 6 min with 9-s access to wheel running as reinforcement. Hatch marks indicate reinforcer delivery. The recorder stopped during reinforcer delivery.

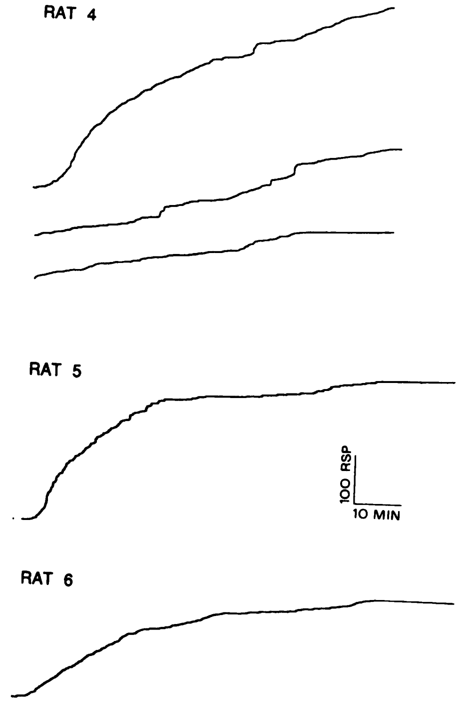

Fig. 7. Cumulative records of lever pressing in extinction after FI 6 min with wheel-running reinforcement. Sessions ended after 15 min without lever pressing. For Rat 4 the record is cut into three segments, with the upper being the first.

reinforcer than under the FR 20 used in Experiment 1 (especially for Rat 4).

Figure 7 shows cumulative records of lever pressing for the extinction session. The session lasted 230, 91, and 93 min, with 653, 303, and 224 responses emitted by Rats 4, 5, and 6, respectively. The beginning of the session was marked by a positively accelerated rate of lever pressing, similar to that seen under the FI 6-min schedule (e.g., Figure 6). As the extinction session progressed, the response rate gradually changed to a negatively accelerated pattern with some occasional increases in local response rate. After approximately 30 min, long pauses began to appear.

Wheel Running

The overall rate of wheel running and the speed of wheel running are presented in Table 3 for free access, FI 10 to 20 s, FI 2 min, FI 6 min (9-s reinforcer), and FI 6 min (5-s reinforcer). (FI 10 to 20 s are chosen to represent initial sessions with wheel running contingent on lever pressing.) For Rat 4, data are also given for FI 6 min with the 15-s reinforcer duration and the replication with the 5-s reinforcer duration.

For all rats, the FI schedule lowered the overall rate of running compared with free access in all conditions. The running speed increased from the small FI size to the FI 6 min with 9-s reinforcer duration for all rats. The running speed increased further for Rat 5 but decreased somewhat for Rats 4 and 6 with the 5-s reinforcer duration. For Rat 4, the running speed decreased slightly at the 15-s reinforcer duration and again at the 5-s replication. However, in all cases the running speed considerably exceeded that with the short FI schedules early in training. The FI schedule did not permit an overall running rate comparable to that in free access because of the restriction in overall reinforcer rate. Under FI 6 min with a 9-s reinforcer duration, for ex-

Table 3

Overall rate of wheel running (revolutions divided by session time, expressed as revolutions per hour) and speed of running during wheel access (revolutions divided by total reinforcer time, expressed as revolutions per second) in Experiment 2. Data are shown for the last three sessions of each condition; for FI 10 to 30 s, one session of each value is shown. Averages are shown, followed by absolute values in parentheses. For FI 10 to 30 s and FI 2 min, the reinforcer duration was 9 s; reinforcer duration is shown in parentheses for the following condition. Running speed is not defined under free access.

Subject	Condition	Overall running rate	Running speed
Rat 4	Free access	265 (242, 269, 283)	—
	FI 10 to 30 s	221 (192, 229, 242)	0.41 (0.34, 0.42, 0.46)
	FI 2 min	129 (126, 120, 143)	0.54 (0.53, 0.51, 0.58)
	FI 6 min (9 s)	78 (71, 77, 86)	0.90 (0.82, 0.89, 1.00)
	FI 6 min (5 s)	35 (35, 40, 31)	0.83 (0.73, 0.81, 0.65)
	FI 6 min (15 s)	111 (117, 114, 102)	0.79 (0.83, 0.79, 0.74)
	FI 6 min (5 s)	37 (32, 43, 36)	0.77 (0.65, 0.92, 0.74)
Rat 5	Free access	188 (197, 165, 201)	—
	FI 10 to 30 s	77 (72, 98, 61)	0.24 (0.20, 0.30, 0.22)
	FI 2 min	67 (50, 82, 69)	0.31 (0.21, 0.39, 0.34)
	FI 6 min (9 s)	29 (23, 36, 28)	0.36 (0.29, 0.43, 0.35)
	FI 6 min (5 s)	21 (21, 19, 24)	0.46 (0.45, 0.43, 0.51)
Rat 6	Free access	103 (107, 90, 112)	—
	FI 10 to 30 s	75 (67, 74, 85)	0.29 (0.27, 0.31, 0.30)
	FI 2 min	85 (66, 88, 102)	0.48 (0.54, 0.51, 0.40)
	FI 6 min (9 s)	40 (39, 35, 46)	0.49 (0.47, 0.44, 0.56)
	FI 6 min (5 s)	19 (22, 19, 16)	0.43 (0.49, 0.44, 0.37)

ample, the highest possible number of reinforcers per hour was 9.75 (3,600/369). For Rat 4, for example, to have regulated running so that the overall rate would approach that obtained under free access, the running speed would have had to be almost three revolutions per second; for Rats 5 and 6, the running speed would have had to be 2.14 and 1.17 revolutions per second, respectively.

Discussion

The FI schedule maintained lever pressing for more than 50 sessions with wheel running as reinforcement. The FI 6-min schedule generated a reinforcer rate considerably lower than that obtained under FR reinforcement in Experiment 1. Experiment 2 therefore extends the results of Experiment 1 by indicating that schedules of wheel-running reinforcement can also maintain operant responding, even when overall running rates are considerably lower than under free access. The pattern of operant responding engendered under FI reinforcement resembled that obtained under FI schedules with food and water reinforcers. For Rat 4, in particular, a positively accelerated pattern of responding, which is characteristic of FI schedules in general (Ferster & Skinner, 1957), was evident under FI 6 min. As in Experiment 1, changes in reinforcer duration did not affect the overall rate of lever pressing appreciably or consistently. The results thus indicate that operant lever pressing could be maintained under an FI schedule of wheel-running reinforcement, even with a relatively short reinforcer duration of 5 s. Although the lever pressing rates were rather low in Experiment 2, responding accumulated over the 6-min interreinforcer intervals occasionally yielded a higher number of responses per reinforcer than in Experiment 1.

Under extinction, the lever-pressing rate decreased gradually without the appearance of the break-and-run pattern seen after FR reinforcement (cf. Experiment 1). With pigeons trained under large FI schedules, break-and-run patterns are evident under extinction. But for rats under FI schedules comparable to those used in the present experiment, the extinction curves are more smooth (e.g., Skinner, 1938), as in the present experiment.

The FI schedule maintained lever pressing even though it prevented the rats from attaining or exceeding the overall rate of running seen under free access to running. The speed of running during reinforcement did increase in Experiment 2, as in Experiment 1, but the speed did not (or could not) increase enough to regulate running to the level of free access. As in Experiment 1, the rat with the highest speed of running (Rat 4) also produced the highest overall rate of lever pressing.

EXPERIMENT 3

The purpose of Experiment 3 was to determine whether lever pressing could be maintained under a VR schedule of wheel-running reinforcement. A variable number of responses produced brief access to running on the wheel. The schedule was increased gradually to VR 20 for 2 rats. To produce a more complex performance involving stimulus control and two response topographies, a chained VR FR was in effect for the 3rd rat. This schedule required a changeover from lever pressing to nose-key responding when the terminal link was in effect. The schedule was increased gradually to chained VR 35 FR 2.

For all 3 rats, sessions were longer than in Experiments 1 and 2 to determine the feasibility of using wheel-running reinforcement in the study of circadian rhythms of operant behavior. The schedules of wheel-running reinforcement were maintained continuously for several days, with food and water available during sessions.

Table 4

The sequence of experimental conditions for Experiment 3. Lever pressing produced access to wheel-running reinforcement under VR schedules for Rats 8 and 9. For Rat 7, the schedule was a chained VR FR, with lever pressing in the initial link (VR) and nose-key responding in the terminal link (FR); the nose key was lighted and a tone sounded in the terminal link.

Subject	Condition	Sessions	Reinforcer duration (s)
Rat 7	Free access	6	—
	Reinforcer control	2	10
	Chain FR 1 FR 1	1	10
	Chain VR 1–5 FR 1	2	10–8
	Chain VR 5–9 FR 2	1	8–6
	Chain VR 10–35 FR 2	16	6
	Chain VR 35 FR 2	8	6
	Chain VR 35 FR 2 (24 hr)	4	6
Rat 8	Free access	2	—
	Reinforcer control	3	15
	FR 1	1	15
	FR 2–5	4	15–10
	VR 5	2	10–8
	VR 5–20	7	6[a]
	VR 20	8	6
	VR 10 (24 hr)	6	6
Rat 9	Free access	1	—
	Reinforcer control	4	15
	FR 1	1	15
	FR 2–5	4	15–10
	VR 5	1	10–8
	VR 5–20	6	6[a]
	VR 20	8	6
	VR 20 (24 hr)	5	6

[a] The reinforcer duration was reduced gradually from 8 to 6 s during the first two sessions of this condition.

METHOD

Procedure

Table 4 shows the conditions of Experiment 3 for each rat. After sessions with free access to running, reinforcer control restricted running to 10- or 15-s periods.

Rat 7. After establishment of reinforcer control, a chained FR 1 FR 1 was in effect for one session. Each lever press turned on a 2000-Hz tone and lighted a nose key (1 cm diameter) located on the middle of the wall, 15 cm above the running surface; a single press on the nose key produced 10-s reinforcer access and turned off the stimuli. Because both lever pressing and nose-key pressing had occurred sporadically during prior sessions, shaping of either response was not necessary. The initial-link schedule was then changed to VR and increased gradually to VR 35, and the terminal-link schedule was increased to FR 2. The reinforcer duration was reduced gradually from 10 to 6 s.

Rats 8 and 9. FR 1 for lever pressing was in effect for one session. The FR was then increased gradually to FR 5. Next, the schedule was changed to VR and increased gradually to VR 20. The reinforcer duration was reduced gradually from 15 to 6 s.

Each rat was kept in the apparatus for several successive 24-hr periods, with the final wheel-running reinforcement schedule continuously in operation for Rats 7 and 9. For Rat 8, the wheel-running schedule was reduced to VR 10. Food and water were accessible during these sessions. Water was freely available from the spout; water drinking was recorded with a custom-made drinkometer system. To monitor food consumption, 45-mg Noyes pellets were delivered contingent upon contact with

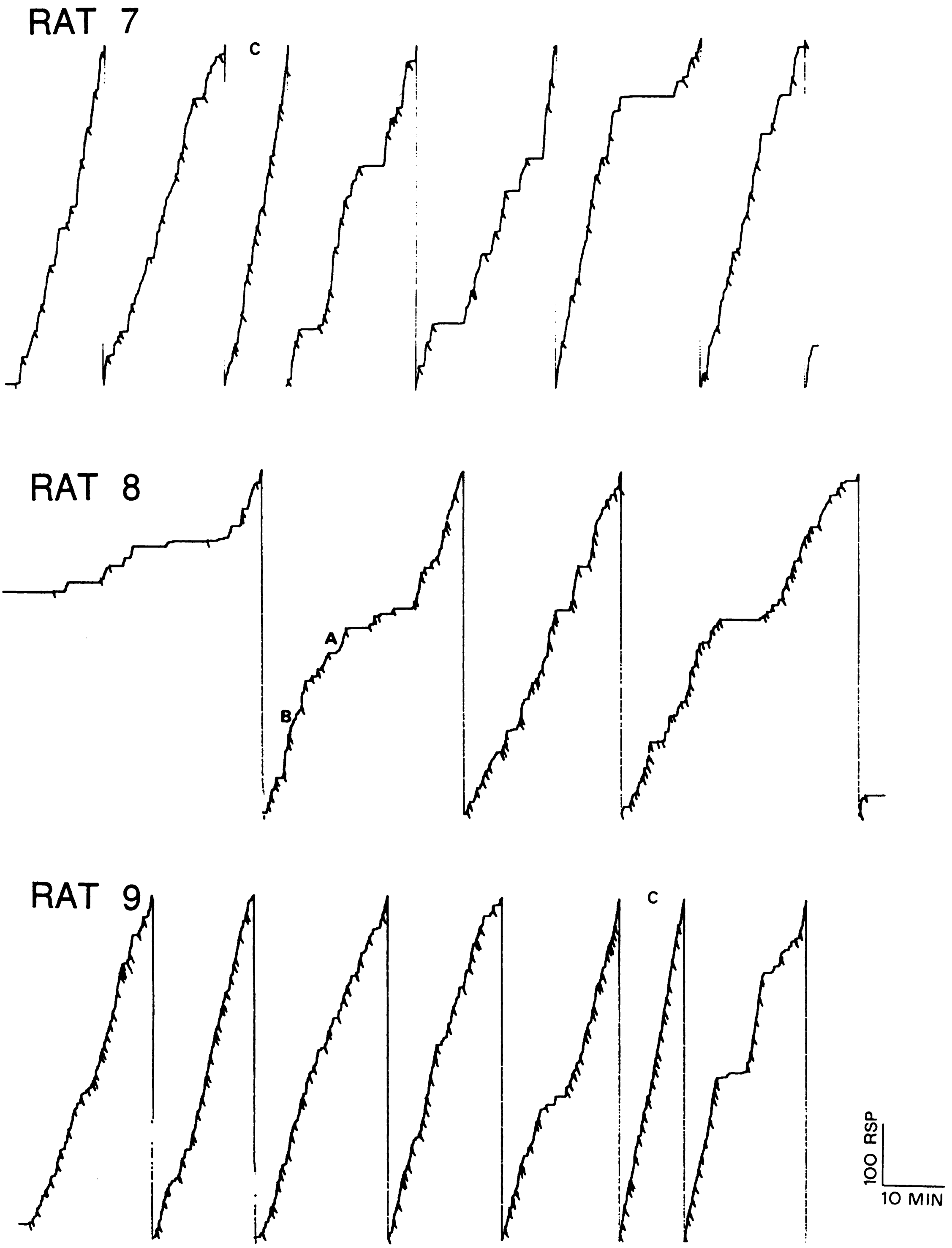

Fig. 8. Cumulative records of lever pressing under VR 20 for Rats 8 and 9 and chained VR 35 FR 2 for Rat 7. Lever pressing was reinforced with 6-s access to wheel running. Hatch marks indicate reinforcer delivery. The recorder stopped during reinforcer delivery. (For Rat 8 the stepping pen was not reset at the beginning of the session by mistake.)

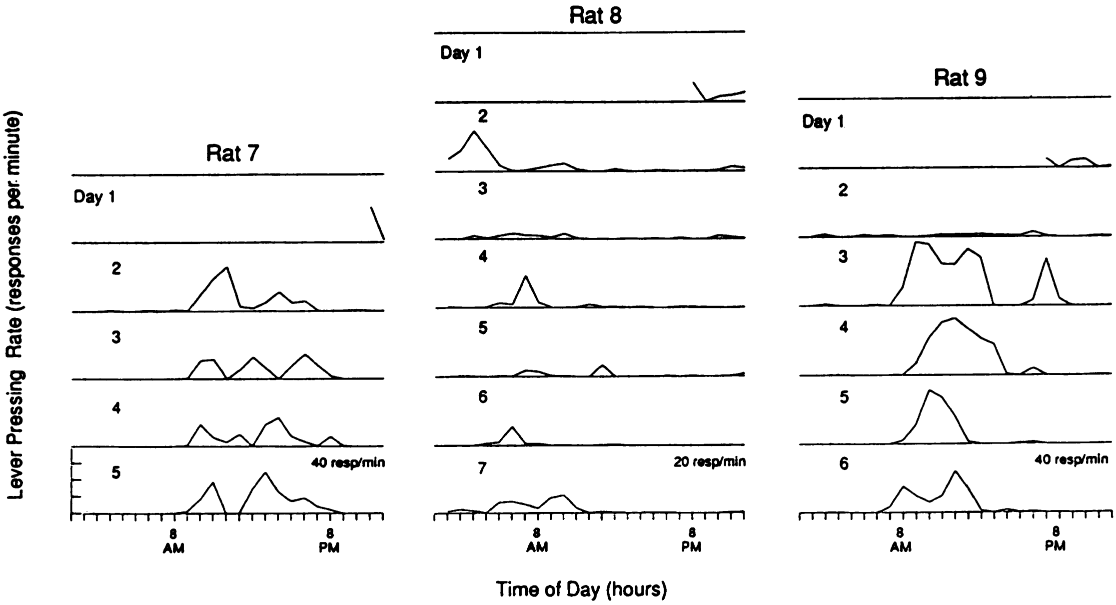

Fig. 9. Rate of lever pressing (responses per minute) for each hour of the day during successive 24-hr sessions. For each rat, lever pressing was reinforced by access to wheel running under VR 35 (Rat 7), VR 10 (Rat 8), or VR 20 (Rat 9). For Rat 7, the VR 35 was the initial link in a chained VR 35 FR 2 schedule; the FR component was pressing a lit nose key. Water was freely available during sessions. Touching the food cup presented food under an FR 10 schedule. To avoid cluttering the graph, the y-axis scale is shown only for Day 5 for Rat 7. The lines separating days form the beginning and end of the y axis for each day. For Rats 7 and 9, the y-axis scale is 0 to 40 responses per minute each day; for Rat 8, the y-axis scale is 0 to 20 responses per minute. Rats were placed in the apparatus in the evening of Day 1.

the food cup; food-cup contact was recorded with a custom-made touch sensor. Food pellets were delivered under an FR 10 schedule; 10 touches on the food cup produced a single food pellet. In the first session with food available during sessions, approximately 50 pellets were placed in the food cup at the beginning of the session. This proved to be sufficient to establish cup contact as an operant food-reinforced response even though the rats were not food deprived.

The rats were placed in the wheel during the evening of the day before the continuous 24-hr sessions. No light was provided in the experimental apparatus (except for the brief nose-key light for Rat 7). The apparatus was cleaned and water and food were replenished (in dim light) once at a different time each day without removing the rat.

Results

Lever pressing was easily acquired and maintained under the VR schedule of wheel-running reinforcement. The VR 20 schedules maintained lever-pressing rates of 9 to 17 responses per minute for Rat 8 and 19 to 35 responses per minute for Rat 9 during the last three 2-hr sessions. For Rat 7, with the chained VR 35 FR 2 schedule, the range was 17 to 34 responses per minute. For Rat 7, the chained schedule exerted appropriate control of lever pressing and nose-key responding; when lever pressing produced onset of the tone and lighted the nose key, the rat quickly (within 1 s) changed to nose-key responding. In the absence of tone and light, nose-key responding occurred at a rate of about 5 to 10 responses per hour.

Figure 8 presents representative cumulative records of lever pressing for each rat. For Rats 7 and 9, the pattern of responding was a relatively steady pace, with only occasional pausing after reinforcement. For Rat 8, however, the record was uneven, with considerable pausing and both positive and negative acceleration between reinforcements (A and B in Figure 8). The local lever-pressing rate (defined here as one full excursion of the stepping

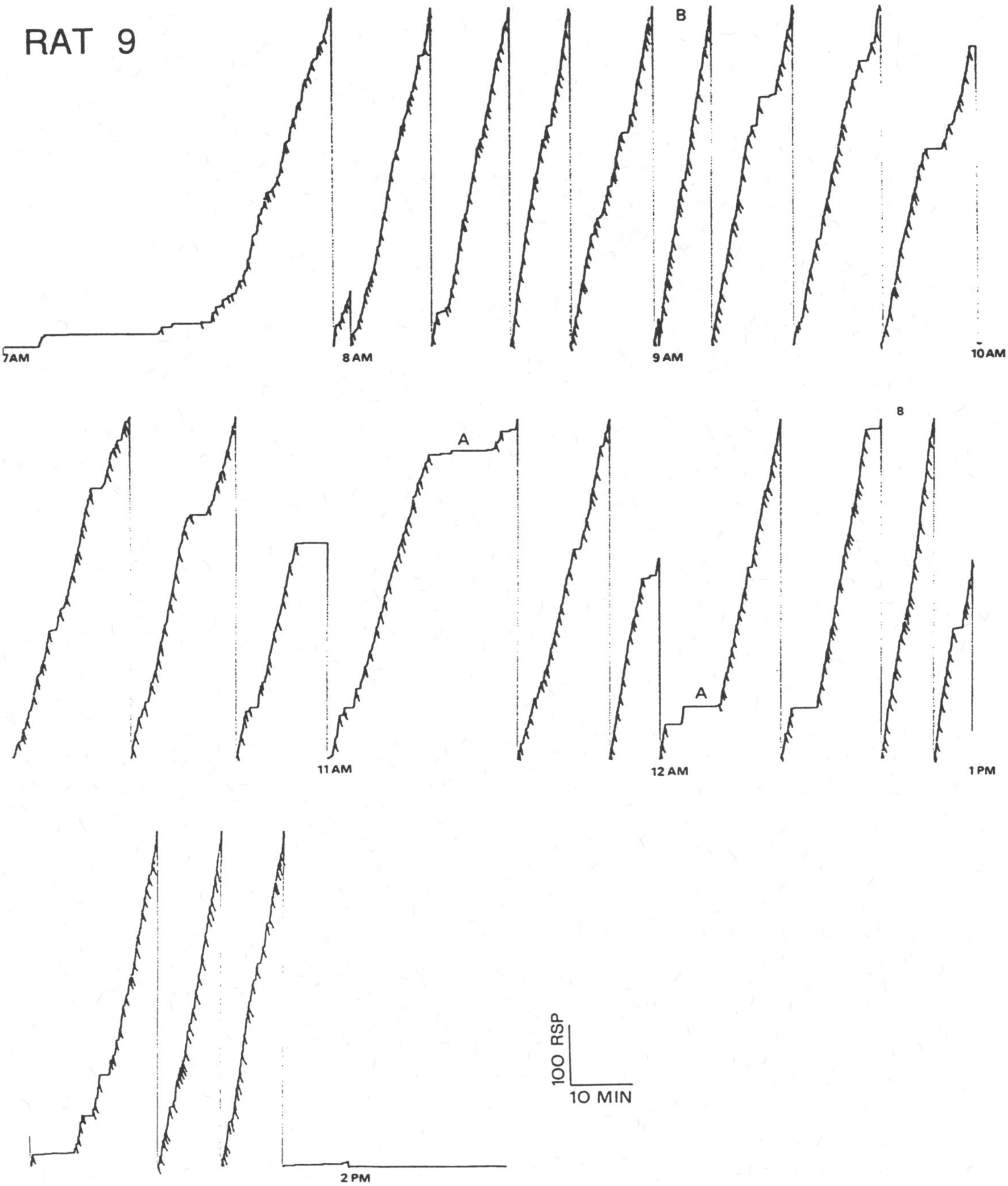

Fig. 10. Cumulative record of lever pressing maintained under a VR 20 schedule of wheel running reinforcement for Rat 9 on Day 3. The record shows a segment of lever pressing that began at about 7:30 a.m. and continued to about 1:50 p.m. Hatch marks indicate reinforcer access. The stepping pen reset at each full excursion (550 presses) and at each hour. The recorder stopped during reinforcer access.

pen on the cumulative recorder, 550 responses, over its time) was occasionally as high as 50 lever presses per minute for Rats 7 and 9 (C in Figure 8).

In the last condition of the experiment, operant responding was monitored in continuous 24-hr sessions. Figure 9 presents lever-pressing rates for each hour of these sessions. (For

Table 5

Overall rate of wheel running (revolutions divided by session time, expressed as revolutions per hour) and speed of running during wheel access (revolutions divided by total reinforcer time, expressed as revolutions per second) in Experiment 3. Data shown for free access are the absolute numbers for the last three sessions for Rat 7 and for each session for Rats 8 and 9. Data for the initial schedules are three sessions with FR 1, 2, and 3 for Rats 8 and 9 and one session of chained VR 1 to 5 FR 2 for Rat 7. Under VR 20 and chained VR 35 FR 2, data are shown for the last three sessions. For the continuous sessions, running speed is shown for each full day. Running speed is not defined under free access. Reinforcer durations were 10 s under initial schedules and 6 s in the remaining conditions.

Subject	Condition	Overall running rate	Running speed
Rat 7	Free access	458, 533, 704	—
	VR 1 to 5 FR 2	256	0.38
	VR 35 FR 2	167, 156, 172	0.82, 0.77, 0.80
	VR 35 FR 2 (24 hr)	(see text)	0.80, 0.92, 0.87, 0.81
Rat 8	Free access	188, 139	—
	FR 1, 2, 3	132, 63, 61	0.24, 0.25, 0.25
	VR 20	25, 32, 28	0.26, 0.30, 0.27
	VR 10 (24 hr)	(see text)	0.24, 0.22, 0.28
			0.33, 0.22, 0.30
Rat 9	Free access	159	—
	FR 1, 2, 3	36, 96, 35	0.12, 0.22, 0.23
	VR 20	139, 162, 143	0.46, 0.47, 0.54
	VR 20 (24 hr)	(see text)	0.34, 0.46, 0.42
			0.54, 0.40

Rats 7 and 9, the scale of lever-pressing rate is 0 to 40 responses per minute each day; for Rat 8, the scale is 0 to 20 responses per minute.) The rats were placed in the equipment during the evening of Day 1. A temporal pattern of responding developed over the following days.

For Rat 7, lever pressing began between 9 a.m. and 10 a.m., then oscillated between high and low rates for the next several hours and ended before 9 p.m.; practically no lever pressing occurred between 9 p.m. and 8 a.m. For Rat 8, the overall level of responding was considerably lower than that for Rats 7 and 9. Also, the temporal pattern of responding was less pronounced. Responding generally began between 2 a.m. and 4 a.m.; very little responding occurred after 1 p.m. For Rat 9, responding occurred at an unusually low rate on Days 1 and 2. In the following days, responding occurred at a high rate between 7 a.m. and 4 p.m. Except for Day 3, responding occurred at a very low rate or not at all after 4 p.m.

The highest lever-pressing rate obtained during 1 hr over all days was 25.9, 9.3, and 36.9 responses per minute for Rats 7, 8, and 9, respectively. Figure 10 shows Rat 9's cumulative record of lever pressing obtained from 7 a.m. to 2 p.m. on Day 3. Lever pressing occurred practically continuously from 7:30 a.m. to 1:50 p.m. at a stable pace with only a few pauses; the longest pause was 5 min (A in Figure 10). On a few occasions, the local lever-pressing rate (as defined for Figure 8) was 65 to 70 responses per minute (B in Figure 10). In the segment shown, a total of 11,400 lever presses occurred, yielding 570 reinforcers. After initial adjustment to the 24-hr sessions, lever pressing thus showed a clear periodicity by occurring in a quite predictable pattern for each rat each day.

During the 24-hr sessions, each rat maintained a daily food intake of about 20 g and a water intake of about 25 mL. In contrast to lever pressing (and running), eating and drinking occurred with a less pronounced temporal patten and were more spread out over the 24-hr sessions. This pattern of eating and drinking is consistent with previous findings in rats under similar constant (dark) lighting conditions (e.g., Collier, 1982). Data on eating and drinking from the present experiment will be presented elsewhere.

Wheel Running

Table 5 gives the overall rate of wheel running and the speed of running during wheel access. Initial schedules of the contingency between lever pressing and wheel-running access are represented by chained VR 1 to 5 FR 1 for Rat 7 (one session) and FR 1, 2, and 3 (three sessions) for Rats 8 and 9. Data are shown for the last three sessions under VR 20 and chained VR 35 FR 2 and for each day with continuous sessions. Overall rate of wheel running is not given for the continuous sessions because session duration is not defined by bringing the subject to and removing it from the equipment, as in previous conditions.

Overall running rate did not reach that during free access under any conditions with the wheel-running schedule for Rats 7 and 8. For Rat 9, the overall running rate under VR 20 was similar to that under free access; however, only one session with free access was given, so a comparison is not entirely valid.

Running speed approximately doubled from initial contingent schedules to final schedules for Rats 7 and 9. For Rat 8, running speed did not increase reliably over the course of the experiment. Notice that for Rat 8, lever-pressing rates could not be maintained as reliably as for the other rats (i.e., Figures 8 and 9).

Discussion

The VR schedule maintained lever pressing for all 3 rats and produced overall lever-pressing rates comparable to those established in Experiment 1 with FR schedules (the FR 20 and VR 20 may be compared directly). The pattern of responding under the VR schedule was a relatively steady pace resembling that obtained under VR schedules with more conventional reinforcers (e.g., Ferster & Skinner, 1957). Wheel-running reinforcement was also able to maintain performance under a chained schedule (VR FR) with two different response topographies, lever pressing and nose-key responding (in effect only for Rat 7).

When sessions were scheduled continuously over several days, operant responding settled quickly into a periodic pattern characteristic for each rat (in particular for Rats 7 and 9). Especially noteworthy was the performance of Rat 9, because lever pressing was maintained almost continuously in 5- to 6-hr blocks on some days. Experiment 3 shows that operant lever pressing can be maintained with wheel-running reinforcement without any deprivation of running other than the local deprivation engendered by the contingency between lever pressing and running.

In the present experiment, lighting conditions were not explicitly controlled, and sessions were conducted in darkness (except for Rat 7 when the nose key was lighted in the terminal link prior to wheel-running reinforcement). Nevertheless, the quick settling of periodicity in lever pressing suggests that the VR schedule of wheel-running reinforcement may be useful in the study of variables that affect the circadian pattern of operant behavior.

The speed of wheel running during reinforcement increased over the course of the experiment for Rats 7 and 9. For Rat 8, running speed did not change and lever-pressing performance was not as well maintained as for Rats 7 and 9. Therefore, the results confirm the trend, seen in the previous experiments, that the most stable and reliable patterns of lever pressing occur for rats that develop a fast running speed during access to the wheel.

GENERAL DISCUSSION

The present experiments demonstrate that lever pressing can be acquired and maintained under schedule control when the reinforcer is wheel running. Operant lever pressing was maintained under FR, FI, and VR schedules with relatively short (4 to 6 s) durations of access to wheel running serving as individual reinforcers. Lever pressing occurred in stable and schedule-appropriate patterns over 2-hr sessions for most subjects. In Experiment 1, an FR schedule controlled a break-and-run pattern in all 3 rats, and for 2 rats lever pressing occurred in a stable pattern throughout each session. In Experiment 2, an FI schedule controlled a positively accelerated lever-pressing rate between reinforcements for 1 of 3 rats, and lever pressing was maintained throughout each session for all 3 rats. In Experiment 3, a VR schedule controlled a relatively steady rate of lever pressing, with only few pauses for 2 of 3 rats and a somewhat variable rate for 1 rat. In addition, Experiment 3 arranged the VR schedules in continuous 24-hr sessions with food and water available in the wheel-running equipment. Lever pressing quickly settled into a characteristic daily periodicity, with lever pressing occurring at a predictable time of day for each rat.

In several previous experiments, FR schedules maintained licking or lever pressing with wheel-running reinforcement (e.g., Collier & Hirsch, 1971; Kagan & Berkun, 1954; Mazur, 1975; Pierce et al., 1986; Premack, 1962, 1965; Premack et al., 1964; Tierney et al., 1983). The present experiments replicate and extend this previous work by demonstrating that schedules with wheel-running reinforcement may be used to establish a stable pattern of operant behavior over 2-hr periods (or longer, as in the case of the continuous sessions in Experiment 3). FR and VR schedules generated the highest lever-pressing rates and the most stable and typical pattern of responding. However, the results with the FI schedule (Experiment 2) are noteworthy because lever pressing was maintained with very little access to running (5 s every 6th minute).

Neither food nor water deprivation nor any special arrangements were required for the experiments. A few sessions with free access to running were scheduled for each rat at the beginning of each experiment. However, one session may be sufficient (as for Rat 9) to determine whether a rat runs or not. Bringing wheel running under control of the stimuli that accompany release of the brake was accomplished in a few sessions with a gradually more severe restriction of access to running. In the present experiments, the schedules were incremented gradually and the reinforcer durations were shortened gradually, as well, to prevent possible breakdown or deterioration of established lever pressing that might occur with sudden large changes in schedule parameters.

The amount of wheel running under free access, for a given rat, turned out to be a poor predictor of the extent to which the reinforcement schedule would control lever pressing for the rat. For example, for the rat that ran the most under free access (Rat D in Experiment 1), the FR schedule did not control a rate of lever pressing comparable to that of the other rats, and the rat was removed from the experiment. Conversely, Rats 1 and 9 had some of the lowest rates of wheel running under free access, yet the reinforcement schedule controlled the most reliable pattern of lever pressing for these rats.

The results regarding speed of wheel running during reinforcer access suggest a consistent trend. Considering the present data collectively, the rats that ran fastest during contingent wheel access also established the highest and most reliable rates of lever pressing (i.e., Rats 1, 3, 4, 7, and 9). Speed of running has been an unheeded variable in previous work on wheel-running reinforcement. However, in one previous study, running speed can be calculated for each subject based on the available data. Pierce et al. (1986) used 60-s wheel-access periods to reinforce lever pressing under an FR 20 schedule. Then a progressive FR schedule was in effect in one test session. The rats with the highest running speed emitted the largest numbers of lever presses during this test session, and the rats with the lowest running speed emitted the smallest numbers of lever presses. These data confirm the trend seen in the present experiments suggesting that speed of running may be a critical variable when wheel running is used as the reinforcer.

The gradual reduction in the duration of access to running over the course of the experiments may be an important determinant in the development of high-speed running. Quite possibly the high-speed running seen for some rats toward the end of the experiment (with 4 to 6 s access to running) may not have occurred during free access. Analyses of free-access data from subsequent experiments in this laboratory support this possibility. Tentatively, the data suggest that the wheel-running reinforcer may possibly be "shaped" by the method of a gradually more severe restriction on running. Recorded wheel running may be a composite of different response topographies. The stepwise reduction in access duration may select faster running at each step. Eventually a speed may appear that did not occur or was rare under free access. As indicated above, the collective data indicate that high-speed running may be a more effective reinforcer than low-speed running. Although clearly speculative at this point, the notion of shaping a reinforcer from the subject's own behavior is at least directly testable. One advantage of using wheel running as a reinforcer (an advantage that is not readily available for food reinforcers) is that running speed can be recorded and possibly manipulated.

Wheel-running reinforcement has been used in previous work primarily to answer theoretical questions. However, the present experiments show that wheel-running reinforcement can also be adapted as a technique to establish schedule control of lever pressing over long sessions. The effects of variables such as age, hormones, drugs, or toxins on the acquisition and maintenance (and extinction) of operant behavior may be studied without the use of food or water deprivation. The method of continuous sessions in Experiment 3 suggests that schedules with wheel-running reinforcement may be used as a baseline to study how various variables affect the circadian rhythms of operant behavior. With minor technical modifications, food and water can be delivered under reinforcement schedules as well, so that different responses are controlled by concurrent schedules of food, water, and wheel-running reinforcement. Thus, the method established in the present experiments can be used to complement existing methods used to study circadian rhythms of operant behavior (e.g., Collier, 1987; Terman, 1983).

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