

## **EFFECT OF LIGHT/DARK CYCLE ON WHEEL RUNNING AND RESPONDING REINFORCED BY THE OPPORTUNITY TO RUN DEPENDS ON POSTSESSION FEEDING TIME**

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*Do rats run and respond at a higher rate to run during the dark phase when they are typically more active? To answer this question, Long Evans rats were exposed to a response-initiated variable interval 30-s schedule of wheel-running reinforcement during light and dark cycles. Wheel-running and local lever-pressing rates increased modestly during the dark phase. A second experiment examined the potential role of food-anticipatory activity in this effect by delaying postexperimental session feeding by 6 hr. No increase in wheel-running and lever-pressing rates was observed during the dark phase. This suggests that the effect of light/dark cycle on running and responding for the opportunity to run depended upon food-anticipatory activity.*

Wheel running is a motivated behavior that shows a circadian rhythm and functions as a reinforcing consequence. Although the daily oscillation of running and the reinforcing properties of wheel running are well documented, the implications of circadian rhythms for the investigation of wheel-running reinforcement have not been determined. In the absence of empirical evidence, sessions of responding for running as a reinforcing consequence for rats are assumed best conducted during the dark phase, when rats are active. Underlying this assertion about procedure may be an assumption that the efficacy of an opportunity to run as a reinforcer may be greater when assessed in the phase when nocturnal animals are most active. The objectives of the current study were to determine if rats (a) run at a higher rate during a brief opportunity to run when it occurs during the dark phase and (b) respond for the opportunity to run at a higher rate during the dark phase.

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Numerous studies have shown that rats typically engage in little or no running during daylight hours when they are usually asleep, but they show a marked increase in running rates during the initial portion of the dark cycle that subsequently subsides as the onset of the light cycle approaches (e.g., Bauer, 1990; Edmonds & Adler, 1977; Eikelboom & Lattanzio, 2003; Mueller, Herman, & Eikelboom, 1999; Peng, Jiang, & Hsu, 1980; Stewart, Rosenwasser, & Adler, 1985). For example, Peng and Kang (1984) showed that a greater amount of wheel running occurred in the dark phase during which a larger number of activity bursts, bursts of longer duration, and shorter intervals between bursts occurred. Eikelboom and Mills (1988) measured wheel revolutions over a 24-hr period in male and female rats. Neither sex ran extensively during the day, with the majority of their activity concentrated in the initial periods of the night. Thus, the observation that rats are typically more active during the dark phase of the light cycle is well established.

In addition to being a dependent measure to document circadian rhythms in activity, wheel running has also been studied as a reinforcing consequence. When the opportunity to engage in this behavior is made contingent upon another behavior such as lever pressing, animals make this response to produce the opportunity to run (e.g., Belke, 1996, 1997; Belke & Heyman, 1994; Collier & Hirsch, 1971, Kagan & Berkun, 1954). However, except for Iversen's (1993, 1998), all investigations of wheel running as a reinforcing consequence in rats have occurred during the resting phase of the animals' activity cycle. In Iversen's (1993) study, rats responded on reinforcement schedules (variable ratio for 2 rats; chained variable-ratio [VR], fixed-ratio [FR] for the third) that produced a 6-s opportunity to run as a reinforcing consequence. The operant response was lever pressing for the rats on the VR schedule and a combination of lever pressing and nose poking for the rat on the chain schedule. Access to the reinforcement schedules was continuous over 24 hr under constant dark conditions across 5 to 7 days. Food and water were freely available. Results showed that the rats developed a circadian pattern of responding for the opportunity to run where lever pressing occurred between 8 a.m. and 8 p.m. for 1 rat, between 2 a.m. and 1 p.m. for a 2nd rat, and between 7 a.m. and 4 p.m. for the 3rd. Thus, all 3 rats displayed periodicity in responding for the opportunity to run in the absence of light/dark cues. Presumably, the organization of this periodicity was related to the 12/12-hr light/dark cycle in the colony room that the animals occupied prior to the experiment; however, since the time of onset of light/dark cycle is not provided, this can only be assumed.

If running and responding for the opportunity to run are higher during the dark phase of the light/dark cycle, then what is the basis of this difference? One possibility is that the reinforcing efficacy of an opportunity to run may be greater during the dark phase than during the light phase. Another possibility is that the increase in lever pressing and wheel running may simply be an effect of a general increase in motor activity. However, before this issue can be addressed, a demonstration is needed to show that running rates during a brief opportunity to run and lever-pressing rates vary with light/dark cycle. That was the objective of the first experiment. These measures were predicted to be systematically higher during the dark cycle because rats are nocturnal.

## Experiment 1

### *Method*

*Subjects.* Eight female Long Evans rats obtained from Charles River Breeding Laboratories in St. Constant, Quebec, Canada, served as subjects in this experiment. At the beginning of the first light phase condition following training, the rats were approximately 5 months old. Each animal was housed in a separate polycarbonate cage (480 mm × 270 mm × 220 mm), covered with a steel-wire lid equipped with a food cradle and water apparatus. Each cage was filled with sterilized beta chips and shredded paper towel to serve as bedding. The colony room was maintained at 20°C with a 12-hr light/dark cycle, lights on at 0730 hr. The diet consisted of Prolab RMH 3000 (LabDiet, Richmond, Indiana) lab chow and free access to water. Rats were fed once a day immediately after each running session and were maintained at a target weight of 260 ± 10 g.

*Apparatus.* Experimental sessions occurred in eight wire-mesh activity wheels (three Wahmann and five LaFayette Instruments Model 86041) measuring 350 mm in diameter and 115 mm in width. Each wheel was housed in a sound-attenuated shell (610 mm × 530 mm × 485 mm) equipped with a fan to provide ventilation and to mask extraneous noise. A retractable lever (Med Associates ENV-112) was mounted directly at the 70 mm × 90 mm opening of each wheel and not in a side cage. The lever extended 18 mm into the wheel through the opening and was located 80 mm above the running surface. The force required to close the lever microswitches ranged from 16 to 24 N. Two 24-V direct-current lights mounted at the front and back of the wheel at a height of 175 mm illuminated the wheel chamber. A microswitch attached to the wheel frame recorded wheel revolutions. A solenoid-operated brake was attached to the base of each wheel. When the brake was engaged, a rubber tip on the end of a metal shaft came in contact with the outer rim of the wheel, causing it to stop. Digital DECpc computers interfaced to the wheels through their parallel ports controlled the experimental events and recording of data.

*Procedure.* Before the present experiment, rats had been trained to press levers in the running wheels. This training consisted of 26 days of free running for 30 min each day. After this period, a retractable lever in each wheel chamber was extended, and the opportunity to run for 60 s depended upon a single lever press. With a single lever press, the lever was retracted, the brake was released, and the wheel was free to turn for 60 s. After 60 s, the brake was asserted and the lever was extended. A session ended after 30 reinforcers were obtained. The schedule of reinforcement was changed through the following sequence of VR schedules: VR3, VR5, and VR9. These schedules were in effect for 5, 6, and 10 days, respectively. Rats were subsequently shifted to and maintained on a response-initiated VI (variable interval) 30-s reinforcement schedule 10 days prior to the onset of the present experiment. On this schedule, the schedule interval did not begin to time until the first response following the termination of a wheel-running period or, in the case of the first interval of the session, the first response following the commencement of the session. Throughout this training phase, the lights that illuminated the wheel chambers were on during the session.

With the commencement of the first experimental condition, wheel chamber lights were turned off during the sessions to keep illumination conditions within the wheels constant across variation in the light/dark cycle in the colony room.

In the initial condition, the light/dark cycle in the colony room was set so that the lights would come on at 0400 hr. Sessions occurred at 0700 hr each day, so that the testing occurred 3 hr into the light phase. This time was chosen on the basis of Eikelboom and Mill's (1988) study showing that the highest rate of running during the dark cycle occurred approximately 3 hr into the dark period. Animals were transported at 0700 hr from the colony room to the adjacent experimental room through a short hallway. During this condition, the hallway and the experimental room were illuminated. This condition was maintained for 30 days. After 30 days, the rats were phase-shifted to a new light/dark schedule. The shift resulted in a full reversal of the light/dark cycle in the colony room so that the rats were tested 3 hr into the dark period. The phase shift occurred gradually over 4 days, with shifts of 3 hr each day. In this second condition, the lights in the hallway between the colony room and the experimental room were turned off so that the rats would not be exposed to light while in transit to the experimental room. Three 7-W red lights in the colony room and one in the hallway were used to enable the experimenter to transport the animals to and from the experimental room and also to weigh and feed the rats following the experimental sessions. Similar lighting conditions were maintained in the experimental room. This second condition remained in effect for 30 days. Following completion of this dark period condition, the animals were once again phase-shifted back to sessions occurring during the light period in the manner previously described. During the third condition, subjects were again tested 3 hr after the onset of the light period and remained under these conditions for 30 days. Across all three conditions, animals were fed immediately after an experimental session with an amount of food that would maintain the animals at the target body weight of  $260 \pm 10$  g.

The dependent measures that the computer recorded were lever presses, time spent lever pressing, postreinforcement pause (PRP) duration, and wheel revolutions. The wheel-running rate (revolutions per minute) was calculated by dividing cumulative revolutions by the number of reinforcers per session. A local lever-pressing rate (presses per minute) was computed by dividing total presses per session by the time spent lever pressing. Time spent lever pressing refers to the time between the lever press that initiated the timing of the schedule interval and the press that produced the opportunity to run cumulated over the 30 reinforcers in the session. The mean PRP duration was calculated by dividing the cumulative pause duration by the number of reinforcers per session.

Data from the last 5 days in each condition were compared. A polynomial contrast was conducted to assess for a quadratic trend (i.e., higher in the dark than in the light phases) across the three conditions, and a two-tailed paired *t* test was used to assess data from the two light periods. An alpha level of 0.05 was adopted for all statistical analyses.

## *Results*

Figure 1 depicts wheel-running rates (revolutions per minute) as a

function of the illumination condition for each animal. Visual inspection of this figure suggests that wheel-running rates increased during the dark condition. All rats ran at higher rates during the dark period than during the light periods, although in some cases the increases were modest. On average, wheel-running rates during the light, dark, and light conditions were 37.91, 40.85, and 38.08 revolutions per minute, respectively. A polynomial contrast revealed a significant quadratic trend in wheel-running rates,  $F(1, 7) = 20.23$ ,  $p < .05$ , confirming that wheel-running rates were significantly higher during the dark phase. A paired  $t$  test comparing wheel-running rates in the two light conditions showed that they did not differ.

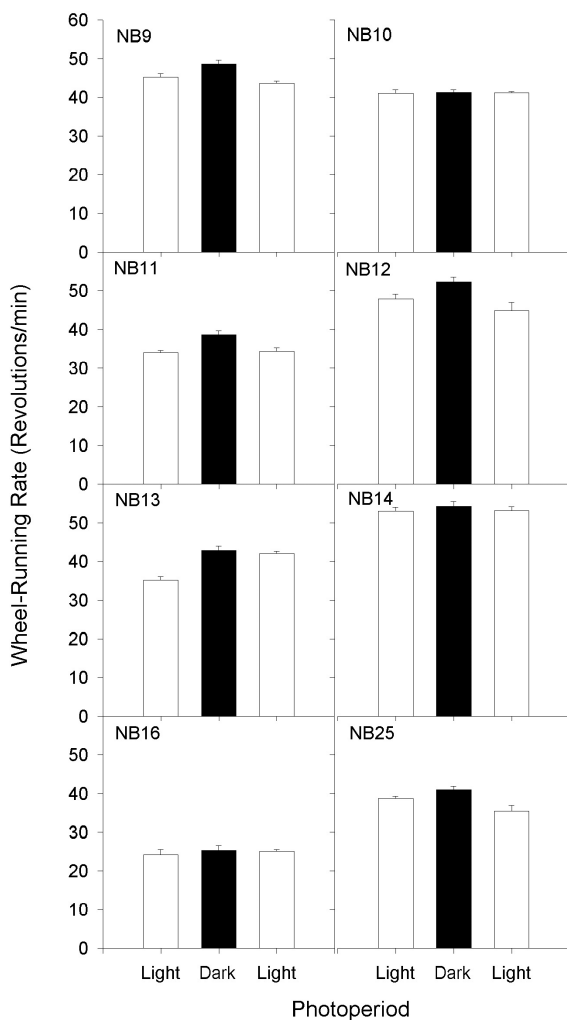


Figure 1. Mean wheel-running rates (revolutions per minute) in the first light, dark, and second light conditions for each rat. In the light and dark conditions, sessions were run 3 hr into the light and dark photoperiods, respectively. Standard error values are plotted for each mean.

Figure 2 depicts mean local response rates (lever presses per minute) as a function of illumination condition for each animal. As with wheel-running rates, this figure shows that local response rates were higher in the dark. Across individual animals, all rats showed an increase in response rates with the shift from the first light to the dark condition; however, only 7 rats showed a subsequent decrease when shifted back to the light condition. For rat NB 16, rates increased monotonically across the three conditions. On average, local lever-pressing rates across the light, dark, and light conditions were 21.96, 26.31, and 22.15 presses per minute, respectively. A polynomial contrast revealed a significant quadratic trend,  $F(1, 7) = 12.30$ ,  $p < .05$ , whereas a paired  $t$  test confirmed that response rates did not differ between light conditions. Thus, lever-pressing rates were significantly higher in the dark phase, but they did not differ between the light phases.

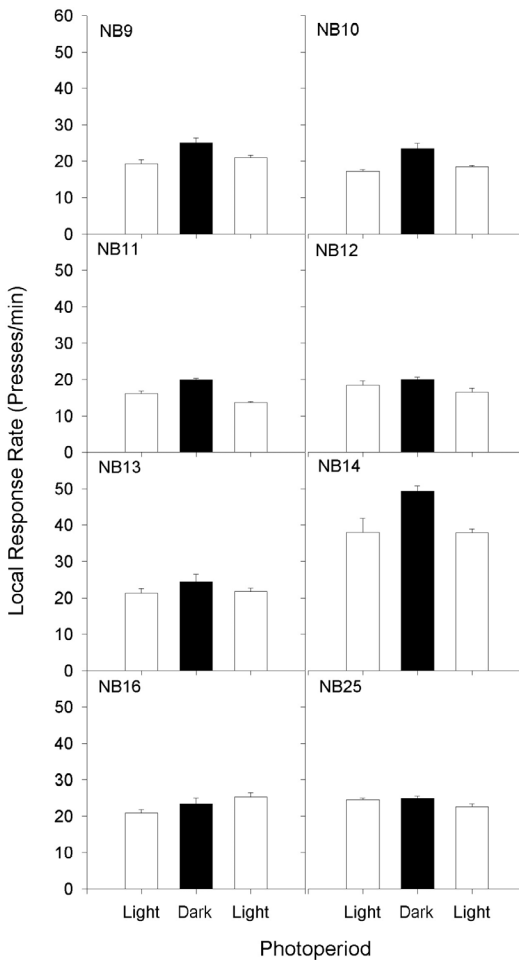


Figure 2. Mean local response rates (lever presses per minute) in the first light, dark, and second light conditions for each rat. In the light and dark conditions, sessions were run 3 hr into the light and dark photoperiods, respectively. Standard error values are plotted for each mean.

Unlike wheel running and local response rates, PRPs did not differ with the illumination condition. Across conditions, pauses decreased, and then increased in 4 rats; increased, and then decreased in 3 rats; and increased in 1 rat. Mean PRPs across the light, dark, and light conditions were 21.35, 21.49, and 22.32 s, respectively. Statistical analysis revealed no effect of the illumination condition. A similar result occurred when median rather than mean PRPs were assessed.

### *Discussion*

As predicted, rats ran at a higher rate during a 60-s opportunity to run when that opportunity occurred during the dark phase. Rats also pressed at higher rates during the dark phase. PRP duration did not vary with the light/dark cycle. These findings are consistent with previous research with wheel running, showing that rats are more motivated to run during the nocturnal period. Although wheel-running and lever-pressing rates increased during the dark phase, the magnitude of the increases was small. Wheel-running rates increased, on average, by 7.8%; and local response rates increased by 19.3%. With respect to wheel-running rates, the magnitude of the increase may have been affected by the rates being near to the upper limit for wheel-running rates. Previous research shows that constraining the duration of the opportunity to run increases wheel-running rates (e.g., Belke, 1997). In the present study, the brief durations of 60 s would have generated wheel-running rates that were high and possibly close to a ceiling in terms of the upper limit for the wheel-running rate. This ceiling would limit the magnitude of increases due to a change in the light/dark cycle.

Although wheel-running rates were high and therefore the magnitude of the effect of light/dark cycle was possibly limited, the same cannot be said for lever-pressing rates. Lever-pressing rates were low relative to local rates generated by other reinforcers such as food. For example, in Belke (2000) on the same reinforcement schedule as in the current study, 0.1 ml of 15% sucrose solution generated an average local lever-pressing rate of 53.49 presses per minute compared with 27.50 presses per minute generated by a 60-s opportunity to run. Consequently, local lever-pressing rates in the present study were not close to a physical maximum, and they could change to a greater degree to reflect an increase in motivation to run. Consistent with this assertion, lever-pressing rates did change to a greater extent than did wheel-running rates; however, the absolute magnitude of the increased lever-pressing rates during the dark period (i.e., 26.31 presses per minute) still falls short of the levels generated by food reinforcement.

An alternative perspective would be that the differences in wheel-running and lever-pressing rates during the dark phase were small, not because of a ceiling effect, but because these rates were already high during the light phase. As stated previously, in most studies of wheel running over 24 hr, little or no running occurs during the light phase. However, in the current study, when sessions were conducted during the light phase, rats readily ran and pressed a lever for the opportunity to run. This suggests that if the opportunity to run is constrained to a very short interval within a 24-hr period, the light/dark cycle has less of an effect than it would if the opportunity to run were not constrained. That is, under constrained conditions, it makes little difference when sessions are conducted.

## Experiment 2

Although wheel-running rates were higher when the experimental session occurred during the dark cycle, the procedure for studying wheel-running reinforcement generated another confound that needs to be addressed: food-anticipatory activity (FAA), which is a form of circadian activity entrained by meal times (Aschoff, von Goetz, & Honma, 1983; Edmonds & Adler, 1977; Honma, von Goetz, & Aschoff, 1983; Mistlberger, 1994; Stephan, 1981, 1992). Specifically, FAA refers to an increase in activity in the hours prior to feeding, whether in the light or dark phase, that occurs under conditions of food restriction. This FAA may be a confounding variable in operant studies. During operant studies of reinforcement, food intake is often restricted to enhance the efficacy of the delivery of a small bit of food as reinforcement during an experimental session. Immediately following an experimental session, or after an interval of 20 to 30 min to prevent handling from being associated with access to food, animals are typically fed an amount of food to maintain the animals at a target body weight level. Thus, the assessment of the effect of a reinforcing consequence on behavior overlaps with the time period during which FAA would occur. This is of particular concern for wheel-running reinforcement for two reasons. First, the opportunity to engage in an activity functions as a reinforcer as opposed to the opportunity to consume food. Second, wheel running is an activity that is typically used to study FAA.

Since the effect of light/dark cycle on running and responding for the opportunity to run was assessed in rats that were food restricted and fed immediately after an experimental session, FAA may have played a role in the results of Experiment 1. Specifically, a light/dark cycle may have interacted with FAA to produce the observed increases during the dark cycle, and therefore the effect can not be attributed solely to the light/dark cycle. To assess this possibility, the effect of light/dark cycle on running and responding for the opportunity to run was assessed with postsession feeding delayed by 6 hr.

### *Method*

*Subjects.* Four female, Long Evans rats obtained from the same source served as subjects in this experiment. The rats were approximately 15 months old at the start of the light-phase condition in this experiment. All other conditions were the same.

*Apparatus.* The experiment was conducted in four of the running wheels (one Wahmann and three LaFayette Instruments Model #86041) described in the apparatus section of Experiment 1.

*Procedure.* The experimental procedure was the same as that for Experiment 1 except that the rats were fed 6 hr after completion of the experimental session rather than immediately following it, and the design involved only exposure to the light-phase condition followed by a dark-phase condition.

### *Results*

Table 1 presents mean wheel-running rates, local response rates, mean PRPs, session times, and body weight for each rat in the light and dark conditions with feeding delayed by 6 hr. Paired *t* tests revealed that unlike the



results from Experiment 1, neither wheel-running,  $t(3) = 2.35, p > .05$ , nor local response rates,  $t(3) = 0.88, p > .05$ , differed significantly between light and dark conditions. Mean wheel-running rates in the light and dark conditions were 38.87 and 34.82 revolutions per minute, respectively, whereas mean local response rates were 21.24 and 22.25 presses per minute, respectively. The PRPs, as was the case in Experiment 1, did not differ between conditions,  $t(3) = 1.43, p > .05$ . Mean PRPs were 31.77 s during the light cycle and 25.05 s during the dark cycle. Finally, since wheel-running and lever-pressing rates differ with body weight, it was important to show that body-weight levels did not differ between the conditions. Average body weights for the rats in the light and dark conditions recorded before the animals entered the wheel were 260.8 g and 261.7 g,  $t(3) = -2.18, p > .05$ .

*Table 1*  
*Mean Wheel-running Rate, Local Response Rate, PRP, Session Duration, and Body Weight in the Light and Dark Cycle Conditions With Postexperimental Session Feeding Delayed by 6 Hr*

Rat	Wheel-running Rate (rpm)		Local Response Rate*		PRP (s)		Session Duration (min)		Body Weight (g)	
	L	D	L	D	L	D	L	D	L	D
NC1	47.0	40.1	31.9	34.2	12.2	12.1	52.3	52.4	261.0	261.0
NC6	40.0	40.9	26.6	25.2	36.4	38.7	64.4	66.4	260.2	261.0
NC10	32.7	26.8	9.1	12.7	31.7	19.9	78.2	61.2	260.4	262.4
NC17	35.8	31.5	17.3	16.9	46.8	29.5	71.8	62.5	261.4	262.2

*Note.* D = dark cycle, L = light cycle, PRP = postreinforcement pause.

\* Local response rate is expressed in presses per minute.

## Discussion

With postsession feeding delayed by 6 hr, the light/dark cycle had no effect on wheel-running and local lever-pressing rates. This finding suggests that the light/dark cycle effect with higher wheel-running and local lever-pressing rates in the dark cycle observed in Experiment 1 depended upon the experimental session overlapping with the time when food-anticipatory activity would occur. When the experimental session was separated from the time when FAA would occur with the feeding delayed by 6 hr, the phase of the light/dark cycle no longer affected wheel-running and local lever-pressing rates.

These findings are important for another reason. The co-occurrence of the experimental assessment of opportunities to run as reinforcing consequences with the time period when FAA is most likely to occur raises the possibility that previous studies of wheel-running reinforcement that used food restriction and postsession feeding (not all do—see Iversen, 1993, 1998) may be assessing the reinforcing efficacy of FAA rather than wheel running in general. To the extent that wheel running under these conditions represents FAA rather than the more general behavior, running and responding for the opportunity to run should be affected by delaying feeding. That is, if the wheel running that occurs during an experimental session is FAA, then delaying postsession feeding should lead to the cessation of running and responding for the opportunity to run during an experimental session. Clearly,

this did not occur; thus, it is likely that previous studies of wheel-running reinforcement (e.g., Belke, 1996, 1997, 2000) that used food restriction and postsession feeding were valid studies of wheel-running reinforcement.

To further assess the effect of delaying postsession feeding, data from the two light conditions in Experiment 1 were averaged into a single set of values, and wheel-running and local lever-pressing rates from Experiments 1 and 2 in the light and dark conditions were compared. An analysis of variance with postsession feeding time (immediate, delayed 6 hr) as a between-subjects factor and light cycle (light, dark) as a within-subjects variable was conducted on wheel-running and local lever-pressing rates. The results of the analysis of wheel-running rates showed no significant main effects of postsession feeding time,  $F(1,10) = 0.28$ , not significant (ns), or light/dark cycle,  $F(1,10) = 0.65$ , ns; however, the interaction between postsession feeding time and light/dark cycle was significant,  $F(1,10) = 21.77$ ,  $p < .001$ . Wheel running was higher during the dark cycle when postsession feeding immediately followed an experimental session but not when it was delayed by 6 hr.

The equivalent analysis of local lever-pressing rates revealed no significant effect of postsession feeding time,  $F(1,10) = 0.21$ , ns, and no significant interaction,  $F(1,10) = 2.86$ , ns; but there was a significant effect of light/dark cycle,  $F(1,10) = 7.52$ ,  $p < .05$ . Local lever-pressing rates were significantly higher during the dark cycle (mean = 24.28 presses per minute) than during the light cycle (mean = 21.65 presses/min). In this case, in the second experiment, data from 2 rats that were in the same direction as those for the 8 rats in Experiment 1 produced this significant main effect rather than a significant interaction as was observed for wheel running. Regardless, the lack of a significant difference in the between-subjects effect for either wheel-running or local lever-pressing rates suggests that these rates were comparable whether rats were fed immediately postsession or 6 hr following a session. This finding suggests that the co-occurrence of the time period when FAA would occur with the experimental session did not appreciably affect the absolute level of wheel running and lever pressing.

## General Discussion

As generally assumed, wheel running and lever pressing for the opportunity to run were higher if an experimental session was conducted during the dark phase when rats are normally active. However, the magnitude of the increases relative to the levels observed during the light cycle was small for both wheel running and lever pressing; and more importantly, the conditions under which this assumption holds were limited. As the second experiment shows, the effect of light/dark cycle disappeared when postsession feeding was delayed by 6 hr. The purpose of delaying the feeding time was to ensure that the experimental session did not overlap with a period of increased activity related to the time of feeding (i.e., FAA). Although independent neural oscillators control circadian rhythms in activity and FAA (Coleman, Harper, Clarke, & Armstrong, 1982; Edmonds & Adler, 1977), in this case the effect of the former appears to depend on the presence of the latter.

A limitation of the current study is that although the conditions that produce FAA (i.e., restricted feeding and a single daily meal) were in effect, there was no independent measure of FAA. Thus, FAA is assumed to be occurring despite the lack of a dependent measure to verify its occurrence. Casual

observation is consistent with FAA being present in that the animals were observed to become active prior to the time of day when their experimental sessions were scheduled to occur.

Another limitation was that the procedure for addressing FAA by delaying feeding time by 6 hr created a 6-hr difference in time since the last meal. Rats in Experiment 1 were deprived of food for 23 hr when experimental sessions were conducted, whereas rats in Experiment 2 were deprived of food for only 18 hr. If wheel-running rates vary with the degree of short-term deprivation, then one would expect that wheel-running rates would be higher in Experiment 1; however, they were not.

A different way to address the issue of FAA would be to conduct the experiment with nondeprived rats. Then FAA would be eliminated because access to food would be ad lib. However, just as delaying feeding time by 6 hr created a confound in terms of a difference in time since last meal, conducting the study with nondeprived rats would also generate differences such as lower wheel-running and lever-pressing rates, longer session durations, and, perhaps, fewer animals successfully trained to lever press for the opportunity to run, since body weight is a strong determinant of motivation to run (Belke, 1996). These differences would render the results less comparable to the majority of studies of wheel-running reinforcement that have been conducted with food-deprived rats.

Finally, with respect to limitations, rats in Experiment 2 were approximately 10 months older at the start of the first condition than were rats in Experiment 1. This age difference raises the possibility that the difference in the results of the two experiments may have been related to the age difference rather than the change in feeding time. Although plausible, it is not probable. Previous investigations of the effect of aging on circadian activity rhythms in male Long Evans rats under ad-lib food access conditions show that although levels of wheel running decrease with age, the majority of activity still occurs during the dark phase. Peng, Jiang, and Hsu (1980) showed that between ages 5 and 18 months, the percentage of total daily running that occurred during the dark phase remained at 80% or greater, despite substantive declines in total daily revolutions. In contrast, Dawson, Crowne, Richardson, and Anderson (1987) found that, with male Long Evans rats, the percentage of 15-min activity sampling periods in which rats were active in the dark phase decreased from 80.1% at 70 days of age to 48.9% at 13 months. For the light phase, the percentage of periods with activity increased from 10.9% at 70 days of age to 15.9% at 13 months. Finally, with respect to the current study that was carried out under conditions of constrained access to running and food, wheel-running rates were not significantly lower in the older rats.

The dependence of the effect of light/dark cycle on postsession feeding time is also important with respect to the interpretation of the basis for this effect. Specifically, the interaction favors a motivational rather than a motor account. That is, the increase in wheel running and lever pressing for the opportunity to run during the dark phase could be the result of a general increase in motor activity. Similar effects are observed for psychomotor stimulants (e.g., caffeine) that increase motor activity by acting indirectly on motor systems and not through motivation to be active (Fisone, Borgkvist, & Usiello, 2004). However, the lack of an effect when postsession feeding was delayed and FAA no longer overlapped with an experimental session suggests

that the increase in wheel running and lever pressing during the dark phase when postsession feeding occurred immediately after the session was a motivational effect. The FAA is an increase in motor activity motivated by the scheduled occurrence of food under conditions of food restriction.

Support for the interpretation that the increase in wheel running and lever pressing during the dark phase may be due to a change in motivation to run also comes from previous research with the effect of light/dark cycle on the reinforcing value of food. Bauman (1992) assessed the effects of increasing an FR requirement per pellet from 5 to 320 responses on food intake during light and dark cycles in a closed economy with rats. Results showed that mean obtained pellets decreased less rapidly and to a lesser extent with increases in the response requirement during the dark period. Likewise, increases in response output were greater and more sustained during the dark period. Using a procedure that increased costs in terms of delay between responses on alternative levers rather than responses, Bauman and Kant (1995) again showed that food intake was reduced less rapidly and to a lesser extent with increases in delay during the dark period. From these results, Bauman and Kant concluded that "photoperiod affects the motivational value of food as a reinforcer for instrumental behavior in a closed economy" (p. 1193).

In summary, as expected, wheel running and lever pressing maintained by wheel running were higher during the dark phase; however, this effect disappeared when postsession feeding was delayed by 6 hr. This finding suggests that the observed increases depended upon the conditions that generate food-anticipatory activity— food restriction and a single daily meal. This interaction suggests that the observed increases were motivational rather than motor. The lack of a difference in wheel-running and lever-pressing rates between the immediate and delayed postsession feeding experiments is also important in that it confirms that previous studies of wheel-running reinforcement that used food restriction and immediate postsession feeding were assessing wheel running in general rather than just food-anticipatory activity.

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