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Circadian Pacemaker Control of Feeding in the Rat, at Dawn

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SPITERI, N. J., A. ALINGH PRINS, J. KEYSER AND J. H. STRUBBE. *Circadian pacemaker control of feeding in the rat, at dawn.* PHYSIOL. BEHAV. **29**(6) 1141–1145, 1982.—Previous studies suggest that feeding at dusk is probably dependent on the rat's immediate energy requirements, while feeding at dawn may have an 'anticipatory' function. However, little is known regarding the relative contribution of habit, energy deficits and circadian pacemakers in the expression of feeding behavior. The aim of the present study was to investigate the involvement of, and interplay between, habit, pacemaker synchronization and energy deficits in the occurrence of dawn feeding in rats. Light onset exerts a strong control over the timing of dawn feeding. The motivation to feed at dawn persists even when access to food is prevented during this period, and shows accompanying shifts with changes in light onset. Rats compensate their caloric deficit imposed by food restriction at dawn by eating earlier in the light phase. This feeding probably occurs in response to feedback mechanisms signalling an energy deficit. The rapid shift in dawn feeding with changes in light onset and food restriction, and its quick reappearance after discontinuing food restriction, argue against habit formation as solely responsible for the occurrence and maintenance of dawn feeding. Habit formation does play a secondary role in the maintenance, but occurs within the 'boundaries' set by the pacemaker. These experiments show that the timing and maintenance of dawn feeding are under the control of a circadian pacemaker which can be shifted by light onset only.

Meal patterning   Circadian rhythm   Food availability   Food intake regulation

APART from delineating positive [12] and negative [5] feedback mechanisms in the regulation and control of food intake, current views emphasize the importance of environmental factors [3,10], habits [4,7] and circadian pacemakers [2, 6, 8, 9, 10]. Food intake in the rat shows a day-night rhythm, about 85% of the total intake being ingested in the dark phase [6, 10, 11]. Feeding activity during this phase shows two distinct peaks, one at the beginning (dusk) and another towards the end (dawn) of the night [6, 9, 10, 11]. Each rat shows distinct feeding and drinking patterns, which are repeated from day to day [6,10].

Previous studies suggest that feeding at dusk is probably dependent on the rat's immediate energy requirements, while feeding at dawn may have an 'anticipatory' function [1,6]. Thus, rats augment their energy stores in advance of the light phase—a period of aphagia and sleep. Further, it is suggested that dawn feeding is influenced by a circadian pacemaker, since changes in light onset, but not short food restriction schedules, can alter the timing of dawn feeding [6].

However, as yet very little is known regarding the relative contribution of habit, feedbacks and pacemakers in the expression of feeding behavior. The present experiments are designed to investigate the involvement of, and interplay between, daily feeding habits, pacemaker synchronization to light onset and energy deficits in the regulation and control of the dawn feeding peak in rats.

METHOD

Animals and Housing

Six male Wistar rats, about 90 days of age and weighing 350–414 g, were kept in a quiet room which was well screened from laboratory noise. The rats were housed individually in Plexiglas cages (25×25×30 cm) on wood shavings and were visually shielded from each other. Water was freely available throughout the experiments. Room temperature was thermostatically controlled at +22°C. The animals were kept under a 12 hr light-dark (LD) regime, with lights out at 12:00 hr. Light was provided by an overhead 40 W daylight-type fluorescent lamp. Light intensity inside the cages was the same for all rats and varied between 4 $\mu W \cdot cm^{-2}$ at cage floor level to about 20 $\mu W \cdot cm^{-2}$ at the level of the food hopper. Light intensity measurements were made with a UDT model 40 optometer using a radiometric filter and a foot-candle diffuser. Food pellets (Muracon, Trouw, The Netherlands) were available in metal food hoppers ad lib. Feeding activity was recorded throughout the day-night cycle on an Esterline-Angus event recorder. A rat could gnaw pieces of food through vertical stainless steel bars situated at the front of the hopper. The gnawing and biting of the food pellets caused the food hopper to swing through a shallow angle, thereby closing an electrical circuit, which deflected a pen on the event recorder. Spillage was collected in an undertray attached to the food hopper. The hoppers

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were filled with the food about two times per week, and at different times in the L-phase. Routine maintenance of the cages was carried out during these times. Access to food could be restricted by a slow-moving, horizontally-sliding door situated in front of the food hopper. Door opening and closing was activated by air pressure, and a time-clock controlled the time of day and duration of the deprivation period. Food intake and body weight were measured daily, at random times in the L-phase, unless otherwise stated.

Experimental Procedure

Experiment 1. The rats were given a two-week habituation period in the cages under a 12 hr LD-cycle. During the following 8 weeks, the rats were subjected to the following conditions: Week 1: This was a pre-experimental week. Rats had ad lib access to food and water. The LD-regime was LD 12:12. Weeks 2 and 3: Two weeks with light onset advanced by 2 hours: LD 14:10 (lights off from 12:00 to 22:00 hr). The rats had free access to food and water. Week 4: During this week, the rats experienced daily periodic food restriction during the first 3 hours of the L-phase, under an LD 14:10 regime. This condition was included in order to investigate whether door closure, preventing food access during the first 3 hours of the L-phase, and opening affected the feeding pattern in any way. Weeks 5 and 6: Two weeks with light onset delayed by 2 hours: LD 12:12. The deprivation period was maintained at the same clock time; so that the rats were now deprived for 2 hours in the D-phase and 1 hour in the L-phase (from 22:00 to 01:00 hr).

This condition was included to investigate whether the peak in food intake, once established before a period of food restriction, would shift with a shift in light onset. This would give information on the relative importance of habit formation in the maintenance of the dawn feeding peak. Week 7 and 8: Two post-experimental weeks with continuous access to food and water. The lighting regime was maintained at LD 12:12 (as in week 5 and 6).

Experiment 2. At the end of Experiment 1, the rats were allowed three weeks to habituate to an LD 14:10 lighting regime. Thereafter, during a period spanning 5 weeks, the rats were subjected to the following conditions: Week 1: Pre-experimental week. Food and water were freely available. Weeks 2 to 4: Three weeks with light onset delayed by 2 hours, from 22:00 to 24:00 hr; and with simultaneous periodic food restriction for 3 hours at dawn, from 22:00 to 01:00 hr. The lighting regime was LD 12:12. Week 5: A post-experimental week, with continuous access to food and water, and with light onset advanced by two hours. Thus the lighting regime during this week was LD 14:10.

In Experiment 1 rats were accustomed to food restriction during a specific time of the day (22:00–01:00) before light onset was delayed by two hours. To investigate whether previous experience with food restriction at that time was important for the shift in dawn feeding together with a shift in light onset, food restriction and light onset delay occurred simultaneously in this experiment. This would also give information on the relative importance of habit formation in the maintenance of the dawn feeding peak. Week 5 was included to see whether the dawn feeding peak would reappear on return to free feeding, after rats were accustomed to a period of food restriction at dawn. This may give information on the relative importance of habit in the establishment of the dawn feeding peak.

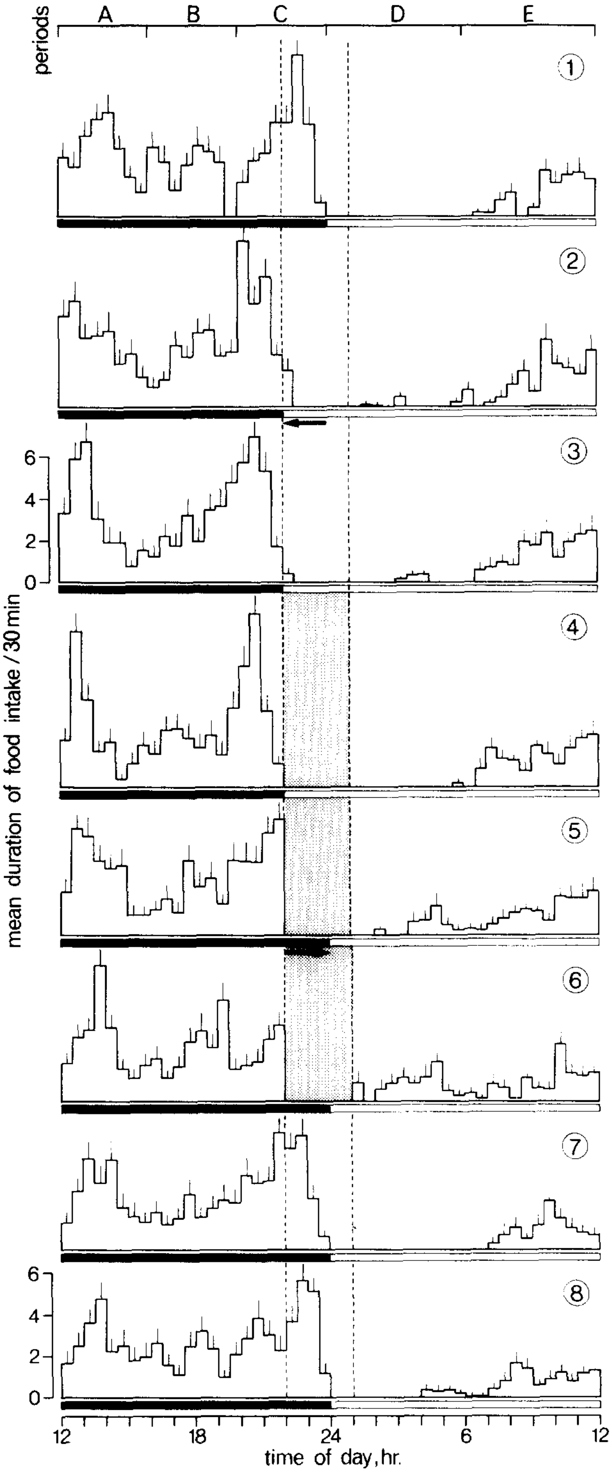

FIG. 1. Experiment 1. Mean duration of food intake per 30 minutes for weeks 1 (control), 2 and 3 (advanced light onset), 4 (periodic food restriction in the L-phase), 5 and 6 (delayed light onset and food restriction), and 7 and 8 (post-experimental weeks). Arrows indicate shifts in light onset. Periodic food restriction at dawn is indicated by the stippled area.

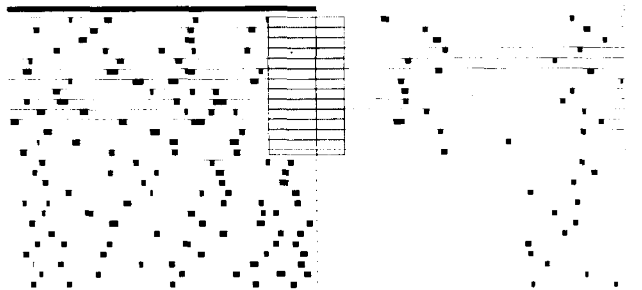

FIG. 2. Diagrammatic representative daily meal patterns of one rat during 14 days of delayed light onset (from LD 14:10 to LD 12:12) in combination with periodic food restriction at dawn (indicated by the stippled area), and 13 days of ad lib food intake. Notice that on return to free-feeding the rat ate immediately in the period in which it was previously deprived of food.

Data Analysis

For each rat, the mean time spent feeding per 30 minutes, over the LD-cycle, was calculated per week. The means±SEM per 30 minutes were then obtained for each week of the experiment, and expressed as histograms (Figs. 1 and 3). For reference purposes, the light and dark phases were subdivided into different time periods. The L-phase was subdivided into two 6-hour periods (D: 24:00 to 06:00; E: 06:00 to 12:00), and the D-phase into three periods of 4 hours each (A: 12:00 to 16:00; B: 16:00 to 20:00; C: 20:00 to 24:00) (Figs. 1 and 3).

RESULTS

Body weight increase and daily food intake were normal throughout both experiments and did not show any significant changes in any of the conditions.

Experiment 1

Light-onset advance. Under LD 12:12, rats consumed about 85% of their daily food intake in the dark phase showing the normal distribution in feeding activity (Fig. 1, week 1). With a change in the light-dark cycle in LD 14:10, by advancing light onset two hours, rats increased their intake during the L-phase to about 20%. Further, the dawn peak in feeding activity shifted to before light onset within one week of the light shift (Fig. 1, week 2); and this peak was re-established by the next week. There was no change in dusk feeding activity (period A).

These results clearly show that advancing light onset results in a shift in the feeding pattern.

Food restriction in the light phase. Depriving the rats of food during the first 3 hours of the L-phase did not alter the feeding pattern significantly (Fig. 1, week 4).

These results show that a three-hour food restriction period, beginning with light onset, does not alter or shift the feeding pattern.

Light onset delay and food restriction at dawn. Delaying light onset by two hours (effectively extending the D-phase by two hours into the deprivation period) caused a significant change in the feeding pattern. The dawn peak in food intake shifted towards light onset (Fig. 1, week 5), and feeding in the 2 hours before food restriction gradually decreased (week 6). By week 6 (Fig. 1) dawn feeding was virtually absent. However, rats ate earlier in the L-phase (week 6, period D). An increase in food intake was also observed in the D-phase, particularly during week 6, period B.

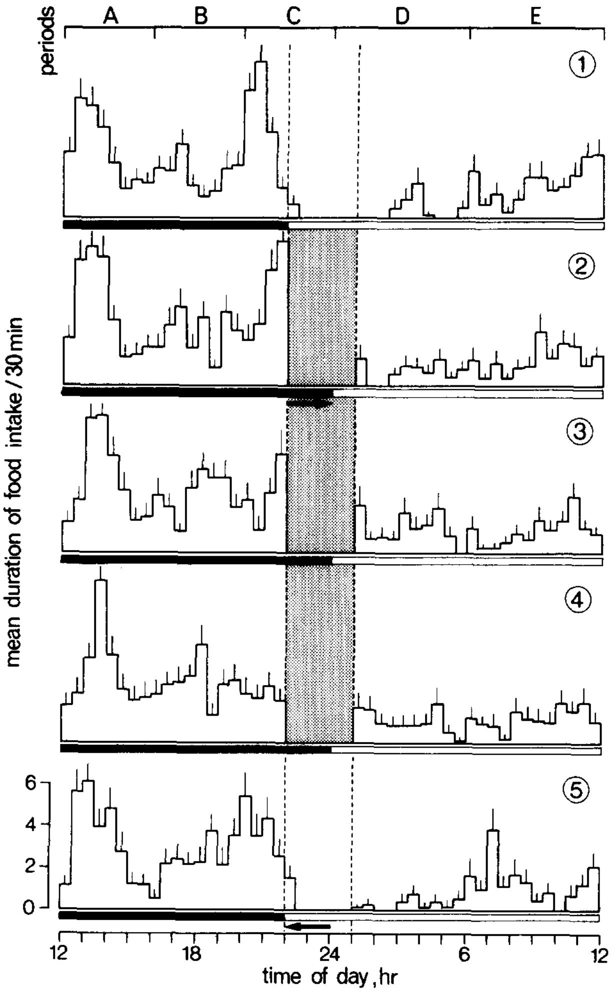

FIG. 3. Experiment 2. Mean duration of food intake per 30 minutes for weeks 1 (control), 2, 3 and 4 (delayed light onset with food restriction at dawn), and week 5 (post-experimental week with advanced light onset, from LD 12:12 to LD 14:10). Periodic food restriction at dawn is indicated by the stippled area.

When ad lib feeding was restored (week 7), dawn feeding returned in the two hours immediately preceding light onset. This occurred during the first post-experimental week. Feeding during the L-phase decreased to pre-experimental levels. Both of these changes can be seen in Fig. 1. Figure 2, a diagrammatic representation of the meal pattern of one rat, shows that on the first encounter with free access to food, the rat ate immediately in the last two hours of the D-phase, and did not eat early in the L-phase. Feeding activity late in the D-phase persisted during the following days. Other rats showed similar changes.

These results show that first, there is a shift in the feeding pattern, such that the decreased food intake late in the D-phase is compensated by an increase in the L-phase, particularly during the 6 hours following deprivation, and around the middle of the D-phase. Second, the rapid increase in food intake late in the D-phase, on continuous access to food, is accompanied by an immediate decrease in food intake in the L-phase, and in the middle of the D-phase.

Experiment 2

During the control week, rats ate about 70% of their daily intake in the D-phase (Fig. 3, week 1). On delaying light onset by two hours (LD 12:12), while simultaneously depriving the rats of food for three hours (from 22:00 to 01:00 hr), the dawn feeding peak shifted gradually towards the new light onset time and decreased in size (Fig. 3, weeks 2 and 3). By week 4, the feeding peak was totally absent at dawn. Feeding activity increased during the dusk period and in the middle of the D-phase (periods A and B). However, rats compensated for most of the decrease at dawn, early in the day (period D).

With a return to LD 14:10 and ad lib food access, the dawn feeding peak was re-established, and feeding activity over the LD-cycle approached normal levels (Fig. 3, weeks 1 and 5).

These results show a shift in the feeding pattern such that the decreased food intake late in the dark is compensated by an increase in feeding early in the L-phase. Other compensatory shifts occur by a decrease in food intake in the second half of the L-phase followed by increased feeding in the first and middle part of the D-phase. Even after three weeks of restricted access to food at dawn, dawn feeding is quickly re-established before light onset on return to continuous access to food.

DISCUSSION

Light onset exerts a strong control over the feeding pattern of rats, so that advancing or delaying light onset is accompanied by changes in the circadian meal pattern, and in particular dawn feeding. Experiment 1 clearly shows that light onset advance shifts the dawn peak in food intake (weeks 1 to 3). This replicates previous findings [6].

Door closure preventing food access in the first 3 hours of the L-phase and opening did not alter the feeding pattern significantly. When the D-phase was prolonged by two hours, while maintaining food restriction during this period, the dawn feeding peak shifted towards light onset (Experiments 1 and 2). This shift resulted in the disappearance of dawn feeding. Dusk feeding also shifted, so that peak feeding activity occurred about one hour later in the D-phase. These results fully support those of a previous study which demonstrates that not periodic food restriction, but advancing light onset shifts the dawn feeding peak [6]. Rats ate earlier in the L-phase, after door opening. This suggests that rats could not bridge the energy gap and may have 'experienced' an energy deficit late in the D-phase and early in the L-phase. It can be argued, therefore, that food intake during the L-phase most probably occurred in response to negative feedback mechanisms registering an energy deficit. On terminating food restriction, rats ate immediately in the two hours preceding light onset (Experiment 1), or in the first hour of light onset (Experiment 2, Fig. 3, week 5). Previously rats had been deprived of food during these periods. Dawn feeding became quickly re-established prior to light onset during the first post-experimental week, in both experiments. These results strongly suggest that the motivation to eat at dawn shifts with changes in light onset, and persists even in the absence of food. The motivation to eat during particular periods in the D-phase also persists when rats are given access to food in the L-phase only [10]. This was still present after one month of diurnal food access. The strength of feeding motivation at dawn can also be seen in Fig. 3. On return to free feeding and simultaneous light onset advance (Experiment 2, week 5), all rats ate during the first hour of the L-phase. It is well known that under normal conditions rats eat little or nothing at all during the first hours of the light period.

It seems that habit plays a secondary role in the expression and maintenance of dawn feeding. With changes in light onset dawn feeding showed a rapid shift, and also reappeared quickly when periodic food restriction was discontinued. Had habit exerted a strong influence on dawn feeding, than one would have expected the persistence of feeding in the period preceding the deprivation period, irrespective of light onset shifts. Conversely, it can be argued that an absence or a slow reappearance of dawn feeding, after its disappearance, would have suggested a major involvement of habit. The rapidity of disappearance and reappearance of dawn feeding argues against this. It is interesting to note that advancing light onset results in a larger shift speed of the dawn feeding peak, then when light onset is delayed. Asymmetries in the rate of phase-shifting during advances and delays in the light-dark cycle is well known [2,8]. Further the shift occurs in the dusk peak as well. Such a difference in shift speed may be ecologically significant. The rats' dawn feeding would shift accordingly with changes in light onset (for example when light onset occurs earlier), thereby minimizing the rat's exposure in the light period to potential predators.

The following tentative explanation may account for the occurrence and maintenance of dawn feeding. A circadian pacemaker, which is entrained to light onset, increases the rat's motivation to feed during the dawn period (in the laboratory, a period of 2 to 3 hours at the end of the D-phase). The timing of meals within this period, for example the occurrence of meals at similar times during successive days, could be due to habit formation but occurs within the 'boundaries' set by the pacemaker. Such a pacemaker could enhance positive feedback mechanisms resulting in larger meals at dawn ([9] and personal observation). That such mechanisms are active during the dawn period is suggested by findings which show that, at dawn, rats eat several meals without immediately digesting them [1]. Thus rats will continue eating on a relatively 'full' stomach. The involvement of feedback mechanisms is suggested by the changes in the feeding pattern in response to a short daily restriction of food intake. Rats show compensatory changes over the light-dark cycle which lead to stable food intake.

Among the entire complex of signals that determine the patterning of feeding, this study evaluates the relative contribution of circadian pacemakers, energy deficits and habits in the occurrence of dawn feeding. These experiments suggest that the influence of the circadian pacemaker is very strong in the timing and maintenance of dawn feeding. Habit formation and energy deficits play a secondary role and occur within the 'boundaries' set by the circadian pacemaker which is synchronized by light-dark changes.

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