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Control by Light of the Temperature Rhythm in Food-Restricted Hamsters

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BORER, K. T. AND K. CLOVER. *Control by light of the temperature rhythm in food-restricted hamsters.* PHYSIOL BEHAV **56**(2) 385–391, 1994.—To establish the relative importance of light and food in the control of core temperature (T_c) rhythm in food-restricted hamsters, mature female hamsters maintained in 14L:10D lighting were fed restricted amounts of food at the onset of light $(n = 6)$ or at the onset of dark $(n = 6)$ and were compared to ad lib-fed animals. After 21–25 days of this entrainment, light stimulus was shifted by 12 h, and animals were kept in shifted lighting for another 13 days. Food restriction led to a 0.6° decrease in the mean T_c, which was expressed entirely during the day in night-fed hamsters and was evenly divided between day and night in day-fed animals. Thus, T_c and general activity rhythms maintained the entrainment to light under both dietary conditions, with peak values for all occurring during the early night. During 13 days following the 12-h shift in lighting, T_c and activity rhythms shifted in all animals, regardless of nutritional status, from entrainment to preceding lighting, through double rhythm frequency, indicating entrainment to preceding as well as current lighting, to entrainment to current lighting. Thus, in food-restricted hamsters, light stimulus rather than predictable timing of food prevails as the entrainer of T_c and activity rhythms.

Activity rhythm   Energy regulation   Oscillators

ANIMALS and man maintain their energy balance by responding to as well as by anticipating their energy needs. Homeostatic mechanisms allow proportional compensatory responses to deviations from energy balance. Rhythmic timing of energy procurement, storage, and utilization anticipates energy needs. Thus, ultradian, circadian, and circannual rhythms provide an intermittent temporal structure to behaviors and processes that also serve to carry out homeostatic regulation of energy balance. A full understanding of a given animal's mechanism of energy regulation requires an analysis of the interactions between the temporal–anticipatory and the homeostatic–compensatory organization of behaviors and processes affecting energy balance.

Among the rodents, the hamster regulates its energy balance in several unusual ways. Hamster feeding behavior appears to be under rigid temporal constraints and to be refractory to homeostatic control. The size of hamsters' meals is not influenced by the state of their energy balance (3). After they have eaten, no additional food is taken during the subsequent 2 h. They fail to maintain energy balance if they can feed every 6 h, but maintain energy balance and compensate for the energy deficits if allowed to feed ad lib (3,4). Compensation for energy deficit is accomplished through a reduction in their resting metabolic rate in proportion to the magnitude of the deficit (4). Thus, hamsters regulate energy balance by physiological means if they are allowed to eat at regular intervals of between 2 and 6 h (3).

Rats also exhibit ultradian feeding rhythm with a 4-h intermeal interval (21), but increase both the frequency of feeding and the size of their meals when food deprived (13,14). Unlike rats,

that eat 80% of daily food at night (25), hamsters consume only about 58% of food at night and 42% during the day (26).

Regulation of core temperature (T_c) is a homeostatic process indicative of the relative contributions of the processes of energy storage and expenditure. Homeostatic control of T_c is manifested through reductions in body temperature when rodents experience body energy losses (2,8,12,16,22). The T_c mechanism also is organized to both respond to and anticipate energy needs. Temporal control over energy expenditure and conservation in the hamster, with light acting as the entraining stimulus, is revealed in higher T_c and physical activity levels during the dark, and in the energy-saving reduction in T_c and activity levels during the light phase of the nycthemeral period.

When food availability is limited, a predictable time of food presentation replaces light as entrainer of T_c rhythm in rats (2,10) and mice (17). The entrainability of T_c, activity, and corticosterone rhythms in the rodents by food (10,15), and its persistence after lesions of the suprachiasmatic nucleus (1,11,18,23,24), in contrast to the loss of light entrainment of these rhythms after the same brain lesions, has led to the inference that two different oscillators may be involved (6). According to this concept, the light-entrainable oscillator controls T_c, activity, and corticosterone rhythms when a circadian light stimulus is present. The other, food-entrainable or anticipatory, oscillator becomes uncoupled from the light-entrainable one and assumes control over these rhythms whenever food acquires high incentive value (1), restricted access to food has a circadian periodicity (1,2,10), or the light entrainment does not operate (6).

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In view of the hamster's rigid temporal control of feeding and its use of proportional homeostatic modulation of heat production to compensate for energy deficits, it was of interest to examine how an energy deficit affects the control of T_c rhythm in this species. During food deprivation, food assumes a high incentive value, and predictable presentation of limited quantites of food at circadian intervals provides the opportunity for the uncoupling of the putative food-entrainable oscillator from the dominant light-entrainable oscillator. We therefore tested the hypothesis that the timing of the presentation of limited quantities of food would substitute for the light stimulus in the entrainment of T_c rhythm as it does in mice (17) and rats (2,10).

To test this hypothesis, we fed one group of hamsters (A) a restricted amount of food early in the day, and provided another group (B) with the same at the onset of night. We compared the T_c rhythm of these two groups to that of ad lib-fed controls. On days 21 and 25 for groups B and A, respectively, a 12-h shift in the lighting was instituted for the remaining 13 days of the experiment to see whether the light or the time of feeding would serve as the entrainer of the T_c rhythm. In addition, we evaluated the changes in T_c level to asses the homeostatic responses to energy deficit and to differences in the time of access to nutrient energy.

METHOD

Animals and Maintenance

Twenty-four female golden hamsters (*Mesocricetus auratus*) were obtained from Harlan Sprague–Dawley breeder (Hazlett, MI). At the start of the experiment, animals were about 50 days old and weighed about 95 g. Animals were housed individually in plastic boxes (20 W, 41 L, and 20 H) with sawdust bedding and wire tops. Water was available ad lib and powdered chow (Purina Formulab 5008) was given (in double glass jars to trap spillage) in ad lib or restricted amounts. Animals were housed in two temperature (23–24°C)- and light-controlled rooms (14L:10D). Lights were on between 0800 and 2200 h for group A hamsters (*n* = 12) and between 2000 and 1000 h for group B hamsters.

Temperature and Activity Measurements

A battery-operated, beeswax-coated radiotransmitter (VM-FH, Minimitter Co, Sunriver, OR), weighing 3 g, was implanted into the peritoneal cavity of each hamster. Transmitters were calibrated before and after use in the experiment, and the radiotransmitter frequencies, which are proportional to T_c, were found to change less than 1% during this interval. A receiver board positioned under the cage collected temperature signals and general activity measurements, which were generated whenever the animal changed its position relative to the two antennas inside the board. Radiofrequencies were transferred to a computer where a Dataquest III program stored T_c and general activity data (arbitrary count units).

Dietary Manipulations

Hamsters were weighed daily. Half of the animals (*n* = 12) received food ad lib and the others received 5–7 g of food daily to produce and maintain about a 20% weight loss relative to ad lib-fed controls. Food restriction was initiated 2 weeks after the transfer of group B to reverse lighting and insertion of radio transmitters. The food-restricted hamsters in both groups were given their daily food ration between 0900 and 1000 h. This took place at the beginning (during the second hour) of the light period for group A hamsters and during the last hour of light preceding

the onset of darkness for group B hamsters. The reversal of lighting during the last 13 days of the experiment also reversed the timing of feeding for the two groups.

Experimental Design

Hamster length between the tip of the nose and the tip of the tail was measured at the time of radiotransmitter implantation by stretching the anesthetized hamster (75 mg/kg of sodium pentobarbital) over a mm scale. Hamsters were matched by weight (94–98 g) and length (16.5–17 cm) and were assigned to four comparable groups. Dietary variables (ad lib vs. restricted) and nycthemeral variables (day-fed vs. night-fed) were applied orthogonally in a 2 × 2 design.

On days 21 (group B) and 25 (group A) of food restriction, the onset of darkness, and consequently the timing of feeding relative to the light stimulus, was reversed for groups A and B during the remaining 13 days of the experiment. Thus, all four groups were subjected to a 12-h phase shift in lighting and the two food-restricted groups were also subjected to a 1-h phase advance (group B) or phase delay (group A) in the timing of feeding.

Statistical Analysis

A repeated-measures factorial ANOVA was used to evaluate weight and mean daily T_c changes in the four groups of hamsters. Scheffe's F-test was used for post hoc comparison of differences among the four groups. A value of $p < 0.05$ was used as a criterion of significance.

The effects of timing of food presentation were evaluated on days 18–19 and 22–23 of food restriction for groups B and A, respectively. A difference score between the T_c of food-restricted hamsters and of their respective ad lib-fed controls was used to assess the relative contribution of light entrainment and homeostatic factors in the control of T_c rhythm. The 24-h day was divided into eight 3-h blocks from the onset of light. These were labelled as A through H for group A [Fig. 3(A)] and I through P for group B [Fig. 3(B)]. The first (blocks A and I) and fourth blocks (E and M) were eliminated from analysis as the time periods during which the variables of light and food availability were changing. The remaining blocks represented four conditions during which different combinations of light entrainment and bioenergetic variables prevailed. At times B, C, and D, hamsters were energy replete in the light phase; during F, G, and H, hamsters were energy depleted in the dark phase; during J, K, and L, hamsters were energy depleted in the light phase; and during N, O, and P, hamsters were energy replete in the dark phase of the photoperiod.

Paired *t*-tests with Bonferroni correction were used to compare the individual 3-h blocks of T_c between groups A and B. Student's *t*-test for independent groups was used to compare individual blocks of groups A and B under corresponding light entrainment and dissimilar bioenergetic conditions (e.g., B vs. J, F vs. N) and under corresponding bioenergetic and dissimilar light entrainment conditions (e.g., B vs. N, J vs. F).

Student's *t*-test for independent groups was also used to compare four 9-h averages of T_c representing different combinations of lighting and bioenergetic conditions (i.e., blocks BCD, FGH, JKL, and NOP) in groups A and B.

A 2 × 2 ANOVA was used to compare changes in the mean T_c in food-restricted and ad lib-fed hamsters during the 8-day period before and the 8-day period after the switch in lighting and to examine the relative effects of nutritional status and time of feeding on the mean T_c and activity levels on days 18–19 (group B) and 22–23 (group A) of food restriction.

The relationship between the T_c and activity was assessed on days 18–19 (group B) and 22–23 (group A) of food restriction with the Pearson product moment coefficient of correlation.

RESULTS

Body weight of restricted hamsters under both lighting conditions became significantly lower than the weights of ad lib-fed controls by day 5 of food restriction, $F(20) = 6.375$, and remained so to the end of the experiment (Fig. 1). There was no difference between the weights of group A and group B hamsters subjected to the same feeding manipulations.

Core Temperature

The rhythmic fluctuations in T_c were evident in all groups of hamsters. Both the ad lib-fed and food-restricted hamsters exhibited a T_c nadir during the early part of the day [periods BCD and IJKL, Fig. 3(A,B)] and a nocturnal T_c peak [periods EF and MN, Fig. 3(A,B)]. There was about a 1.3°C difference between the diurnal T_c nadir and the nocturnal peak in the ad lib-fed hamsters. Day-fed animals in group A also displayed a transient T_c elevation at the time of feeding [period AB, Fig. 3(A)].

In food-restricted hamsters maintained under both lighting conditions, the mean daily T_c became significantly lower on day 7 of food restriction, $F(20) = 14.52$ [Fig. 2(A,B)], at which time their weight deficit relative to ad lib-fed controls was about 9–13% (Fig. 1). The T_c of food-restricted hamsters continued to decline through day 17 (group A) and day 15 (group B) of deprivation, at which time both the body weights (Fig. 1) and T_cs of the two restricted groups stabilized at about 21% and 0.6°C, respectively, below the values of ad lib-fed control hamsters.

The timing of daily feeding in food-restricted hamsters modified the timing of the deprivation-associated T_c decline. Nocturnal T_c elevations of food-restricted hamsters in group B, which were fed during the period M, matched in magnitude T_c peaks of the the ad lib-fed controls during the time blocks M, N, and O [Fig. 3(B)]. They displayed significant T_c decline only during the last or fourth nocturnal block, P. In this group, lowest T_c differences of about 0.5–0.75°C between the food-restricted and ad

FIG. 2. Mean T_c in the ad lib-fed (open symbols) and food-restricted (closed symbols) hamsters during the 37 days of the experiment. The onset of light was switched to 2000 h in group A on day 25 [(A) squares] and to 0800 in group B on day 21 [(B) circles].

lib-fed controls were seen during the diurnal periods J, K, and L [Fig. 3(B)]. Therefore, T_c differences between the food-restricted and ad lib-fed hamsters during the diurnal time blocks J ($t = 5.39$) and K ($t = 6.48$) were significant and greater than the T_c differentials during the nocturnal periods N and O, respectively. In addition, T_c differential for the diurnal 9-h block JKL was significantly different from the T_c differential for the nocturnal 9-h block NOP ($t = 5.913$).

In the day-fed food-restricted hamsters of group A, there was a uniform reduction in T_c averaging between about 0.2 and 0.8°C throughout the 24-h period [Fig. 3(A)]. As a result, T_c differentials between the food-restricted and ad lib-fed hamsters were similar in all comparisons except for that between the fourth diurnal and fourth nocturnal blocks D and H ($t = 3.719$).

The reversal of lighting and feeding times abolished the T_c difference between the groups with different dietary treatments through a significant 0.7°C reduction in T_c of ad lib-fed hamsters in group A and a smaller 0.2°C (NS) T_c increase in food-restricted hamsters [Fig. 2(A) and Table 1). Similar, but smaller and non-
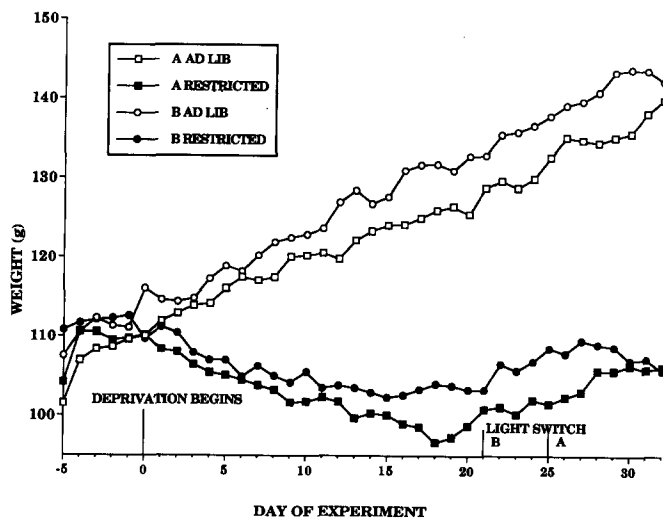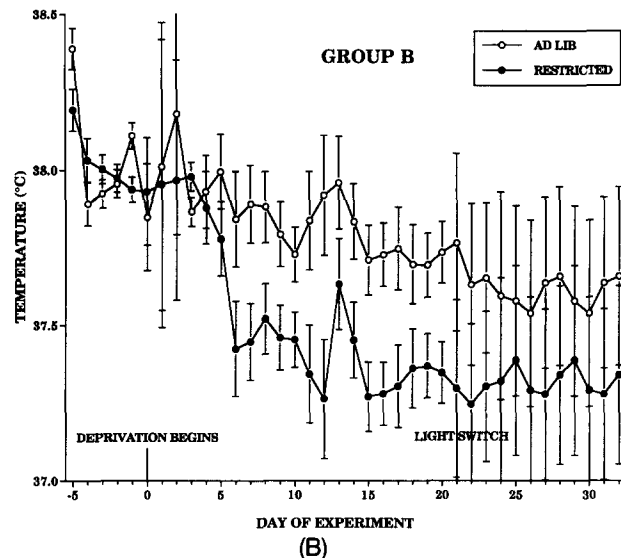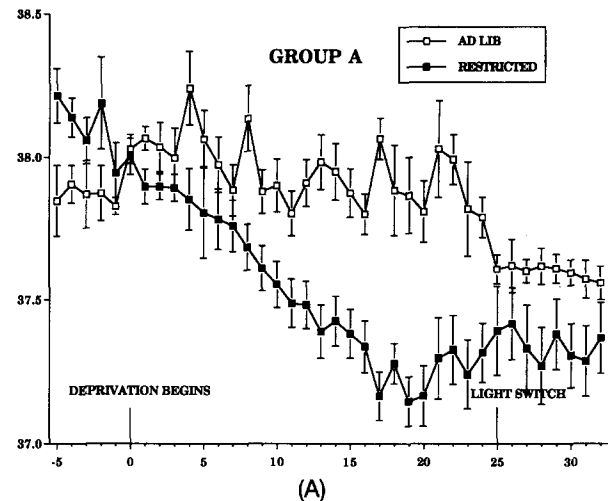

FIG. 1. Mean body weight changes the ad lib-fed (open symbols) and food-restricted (solid symbols) hamsters maintained in 14L:10D photoperiod during 37 days of the experiment. Lights were on between 0800 and 2200 h for group A (squares) and between 2000 and 1000 h for group B (circles).
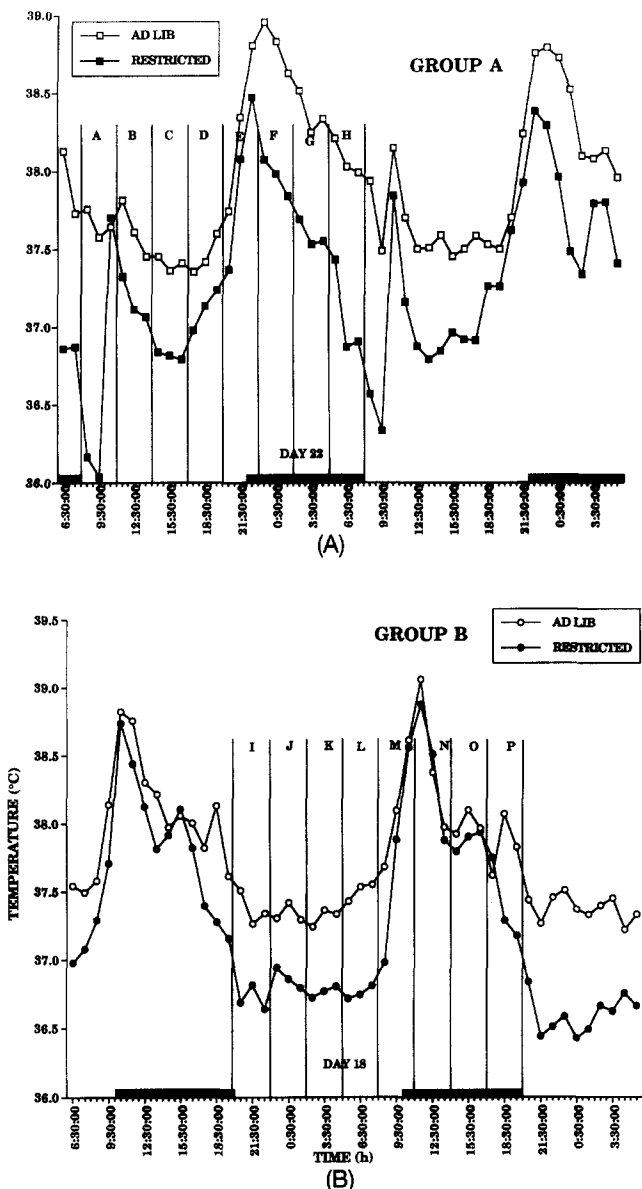
FIG. 3. Nycthemeral T_cs in the ad lib-fed (open symbols) and food-restricted (closed symbols) hamsters are shown for day 22 of food restriction in group A hamsters [(A) squares] and for day 18 in group B hamsters [(B) circles]. The 3-h blocks B–D, F–G, J–L, and N–P were used in statistical evaluation of the data.

General Activity

General activity rhythm of the four groups of hamsters was in phase with the T_c rhythm both before the switch in lighting (Fig. 5) and after (Fig. 6). The 12-h phase shift in lighting led to a doubling of the periods of the activity rhythm (Fig. 6) as the ad lib-fed and food-restricted hamsters made a similar transition from the entrainment to the preceding lighting to the entrainment to the current lighting. Thus, on day 3 after the switch, 12 hamsters displayed inappropriate entrainment of the activity rhythm to the preceding lighting, 10 hamsters had double rhythms, and two were entrained to current lighting. On days 7 and 8 after the shift, the majority of hamsters displayed double rhythms ($n = 17$) (Fig. 6), and the remaining animals were entrained either to the preceding ($n = 5$) or to the current lighting ($n = 2$). On day 13, five hamsters were entrained to preceding lighting, 12 had double peaks, and seven were entrained to current lighting.

There was a small increase in general activity in day-fed food-restricted hamsters at the time of feeding [Fig. 3(A), blocks AB].

Relationship of T_c and General Activity

On days 18–19 [group B, Fig. 3(B)] and 22–23 of food restriction [group A, Fig. 3(A)], food-restricted hamsters had significantly lower T_c and activity levels (Table 2). Nycthemeral variable significantly affected T_c and activity, both of which were significantly higher during the dark than during the light period (Table 2). In addition, there was a significant interaction between the nutritional and nycthemeral variables with respect to the activity level as the ad lib-fed hamsters displayed significantly more general activity during darkness than the food-restricted hamsters (Table 2). During the light phase, there was no correlation between the physical activity and the T_c ($r = -0.25$). During darkness, T_c and activity were significantly correlated ($r = 0.60$, $F = 12.06$, $p < 0.005$).

DISCUSSION

In the present study, we examined the relative importance of temporal and bioenergetic controls over the temperature rhythm in the mature golden hamster. We tested the hypothesis that an energy deficit would override the light entrainment of the circadian temperature rhythm, as is the case in mice (17) and rats (2,10). The entrainability of the daily peak in T_c and activity in the food-restricted hamsters to the time of daily feeding would support the notion of an independent food-entrainable oscillator that can become uncoupled from a light-entrainable one and assume control over the timing of these rhythms (6). In the food-restricted rats and mice, the food-entrainable oscillator is thought

significant, changes in T_c occurred in the hamsters in group B [Fig. 2(B) and Table 1].

In addition, a 12-h phase shift in lighting led to a doubling of the periods of T_c rhythm (Fig. 4) as the ad lib-fed and food-restricted hamsters made a similar transition from the entrainment to the preceding lighting to the entrainment to the current lighting. Thus, on day 3 after the switch, 12 hamsters displayed inappropriate entrainment of T_c to the preceding lighting, and the other 12 displayed simultaneous entrainment to the preceding and current lighting. On days 7 and 8 after the shift, the majority of hamsters displayed double T_c rhythms ($n = 16$) (Fig. 4), whereas the remaining animals were entrained either to the preceding ($n = 3$) or to the current lighting ($n = 5$). By day 13, 10 hamsters were entrained to the current lighting and 14 animals still displayed double rhythms.

TABLE 1

MEAN T_c IN FOOD-RESTRICTED AND AD LIB-FED HAMSTERS DURING THE 8 DAYS BEFORE AND 8 DAYS AFTER THE SWITCH IN LIGHTING

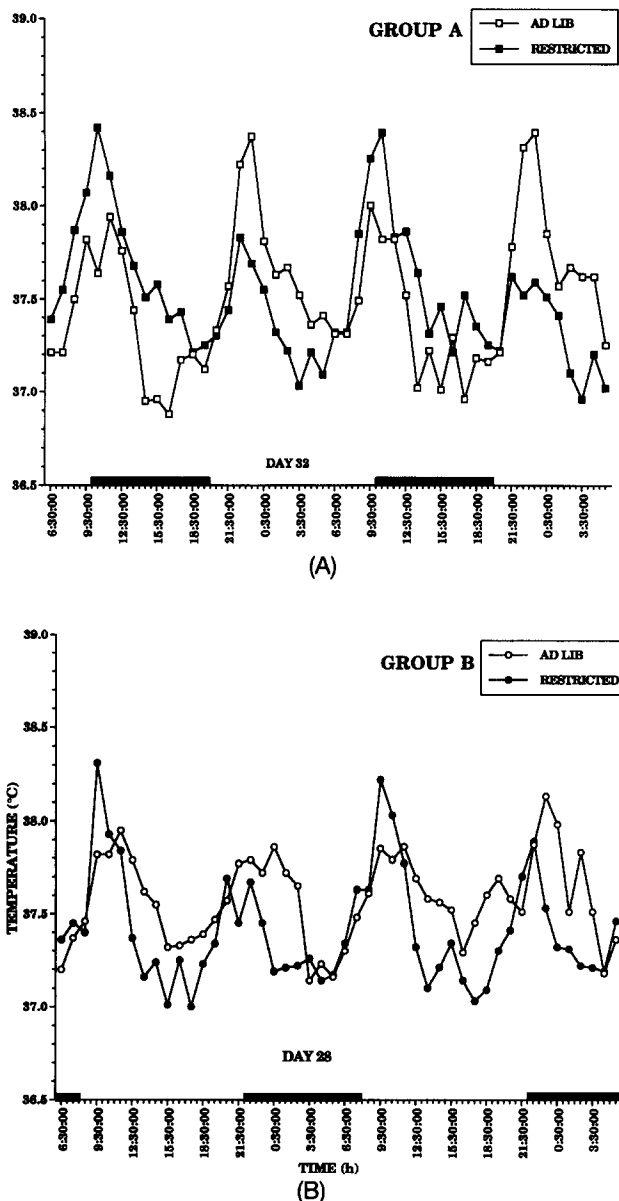|	Ad Lib	Restricted	p
Group A			
Before	37.9 ± 0.1	37.2 ± 0.1	<0.05
After	37.2 ± 0.1	37.4 ± 0.1	NS
p	<0.05	NS	
Group B			
Before	37.8 ± 0.1	37.0 ± 0.1	NS
After	37.6 ± 0.1	37.3 ± 0.1	NS
p	NS	NS	

FIG. 4. Doubling of the T_c rhythms in ad lib-fed (open symbols) and food-restricted (closed symbols) hamsters on days 7 and 8 after the 12-h phase shift in the light stimulus [(A) group A, squares; (B) group B, circles].

to time anticipatory increases in activity and T_c when food ration is presented out of phase with the entraining light stimulus (6). The question of whether, under the restricted feeding conditions, the entrainment of the two rhythms is independent of each other, or whether the T_c rhythm gets entrained to the anticipatory peak of the activity rhythm is of considerable interest (5).

Contrary to our working hypothesis and to the responses in mice (17) and rats (2,10), food-restricted hamsters retained the entrainment of their T_c (Fig. 3) and activity rhythms (Fig. 5) to light regardless of their nutritional status or of the timing of restricted access to food. The prevailing influence of light in the entrainment of the hamster T_c (Fig. 3) and activity rhythms (Fig. 5) is evident from similarity in the appearance of these rhythms displayed by ad lib-fed and by food-restricted hamsters fed at distinctly different times. We found no evidence that the antici-

pation of feeding could assume the role of zeitgeber in food-restricted hamsters, but observed small and transient anticipatory increase in T_c [Fig. 3(A), blocks AB] and in general activity [Fig. 5(A), blocks AB] in food-restricted hamsters at the time of daytime feeding. When food-restricted hamsters were fed at the onset of dark, their anticipatory increases in T_c [Fig. 3(B)] and general activity [Fig. 5(B)] could not be distinguished from the concurrent nocturnal increases in both of these variables. Thus, we saw no evidence of an independent food-entrainable oscillator in food-restricted hamsters fed at regular 24-h intervals. Anticipatory activity and hoarding (1), as well as increases in T_c in response to disturbance and stress (7), have been described in hamsters and could account for the transient increases in T_c and activity that we observed at the time of daytime feeding.
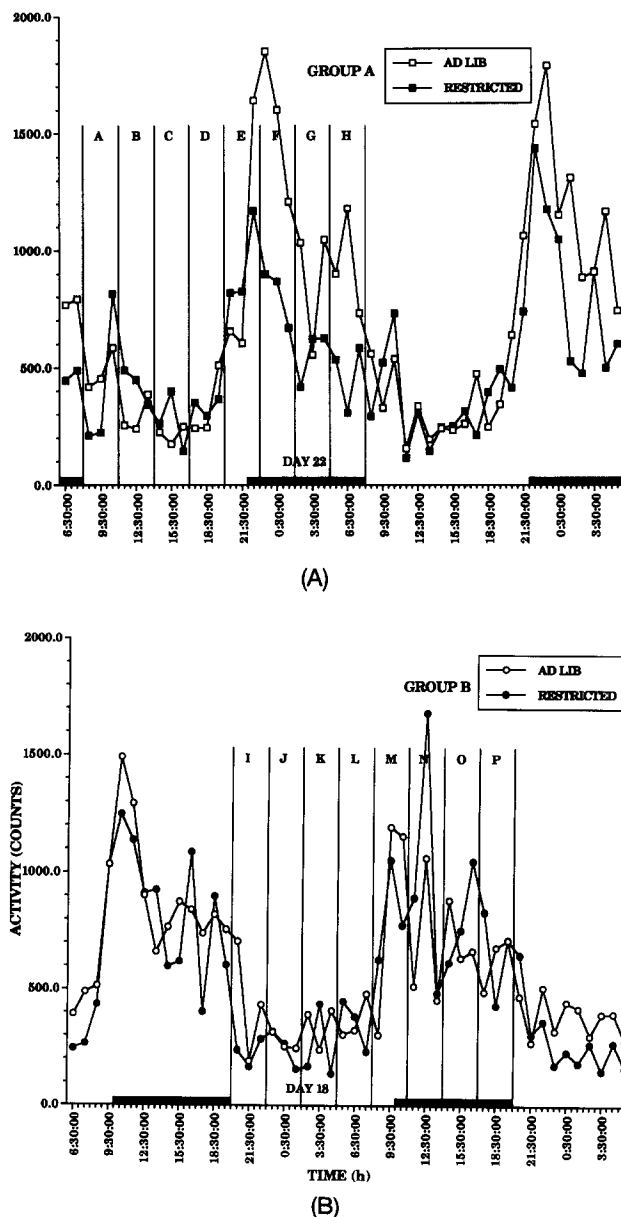

FIG. 5. Nycthemeral activity rhythms of the ad lib-fed (open symbols) and food-restricted (closed symbols) hamsters are shown for day 22 of food restriction in group A [(A) squares] and for day 18 in group b [(B) circles]. The 3-h blocks B–D, F–G, J–L, and N–P are shown for ease of comparison to T_c data.
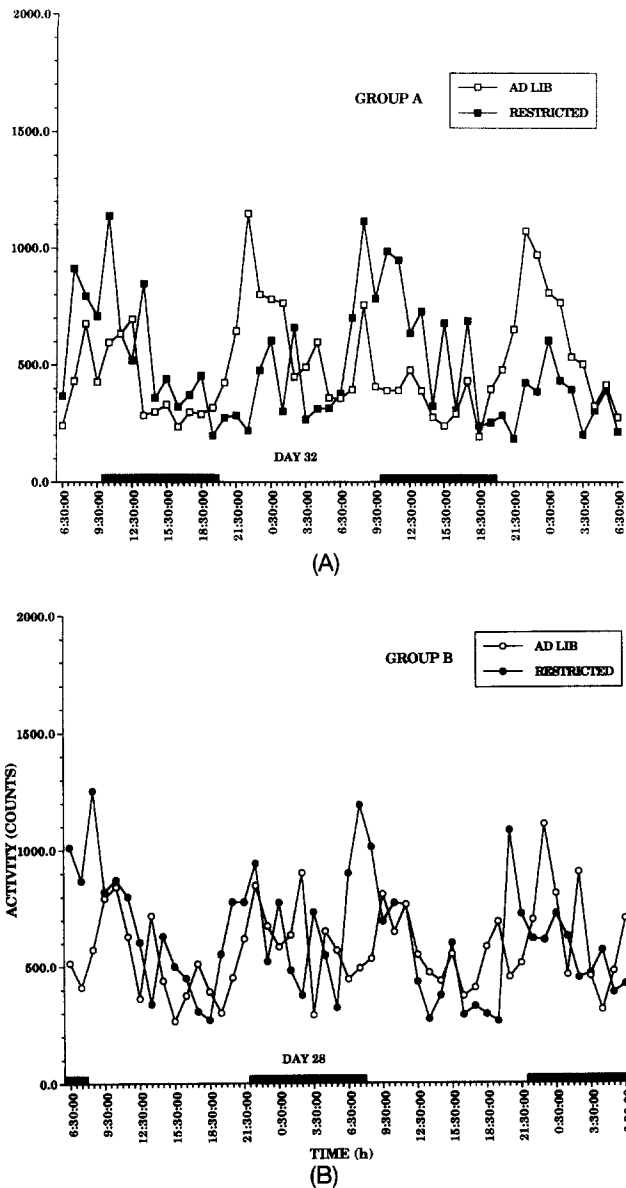
FIG. 6. Doubling of the activity rhythms in ad lib-fed (open symbols) and food-restricted (closed symbols) hamsters of groups A (squares) and B (circles) on days 7 and 8 after the 12-h phase shift in the light stimulus.

The adherence of the T_c rhythm in food-restricted hamsters to light entrainment and its unresponsiveness to fluctuations in nutrient energy is paralleled by the rigid temporal organization of the hamster feeding regardless of the animal's state of energy balance (3). Thus, at least two components of the energy regulatory system in the hamster, the energy procuring behavior and the processes of heat loss through nycthemeral changes in T_c, are subject to relatively inflexible control by endogenous clocks.

Food-restricted hamsters faced with a chronic energy deficit achieved energy savings by reducing their mean daily T_c by 0.6°C (Fig. 2), in agreement with similar observations in other rodents (2,8,12,16,22) and birds (20). This observation is consistent with the previous findings of a homeostatic modulation of metabolic rate in hamsters in proportion to the magnitude of their energy deficit (4). The energy savings that hamsters achieve through a reduction in T_c is more readily expressed during the diurnal phase

of the nycthemeral period [Fig. 3(B)] than at night [Fig. 3(A)]. Hamsters in group B, that experienced the greatest energy depletion during the day, expressed almost all of the decline in T_c during the day and a small amount toward the end of night [Fig. 3(B)]. By contrast, hamsters in group A, which were energy replete during the day, displayed the typical diurnal T_c decline and nocturnal T_c elevation. Their energy savings were achieved by an evenly distributed reduction in T_c throughout the nycthemeral period [Fig. 3(A)]. This suggests that, in the hamster, the homeostatic compensations for energy deficit are carried out mostly through an increase in diurnal energy conservation (group B) and to a limited extent through a modest curbing of nocturnal energy expenditure (group A).

In addition, T_c (Fig. 3) and general activity (Fig. 5) were correlated at night but not during the day (Table 2). This further suggests that during the daytime energy conservation is achieved by maintaining general activity at its lowest level regardless of the hamster's nutritional status, and by a homeostatic reduction in the mean T_c. In contrast, during the dark phase, increases in energy expenditure are achieved through increased physical activity and T_c elevation, and both of these processes can be curbed in proportion to the magnitude of energy deficit.

A 12-h phase shift in lighting led to a doubling of the frequency and to a 50% reduction in the period of temperature and activity oscillations in both ad lib-fed and food-restricted hamsters. Doubling of activity and temperature rhythms is occasionally seen in day-fed food-restricted rodents with one T_c rhythm showing entrainment to the light and the other one to the time of feeding (2,5,9,15). Thus, previous reports of doubling of the activity rhythms could be interpreted as an expression of food-entrainable oscillator operating concurrently with the light-entrainable oscillator. Our observation differs substantially from this pattern in that the doubling of the T_c and activity rhythms is associated with a 12-h phase shift in the time of lighting in both the ad lib-fed and in food-restricted hamsters. Thus, this doubling of the T_c and activity rhythms is triggered by the light shift and is not related to food restriction or the anticipation of feeding. Instead, doubling of T_c and activity rhythms in hamsters subjected to a 12-h phase shift in the onset of darkness most probably represents simultaneous entrainment to both the lighting that prevailed before and the light stimulus prevailing after the phase shift. This inference is supported by the expression in the ad lib-fed as well as in food-restricted hamsters of three stages of transition, from entrainment to the original to entrainment to the shifted light stimulus. These stages were a predominant entrainment to preceding lighting and some double entrainment, followed by a predominance of double entrainment and some en-

TABLE 2

EFFECTS OF THE NYCTHEMERAL PERIOD AND OF THE NUTRITIONAL STATUS ON T_c AND GENERAL ACTIVITY DURING DAYS 22 AND 23 OF DEPRIVATION IN GROUP A AND DAYS 18 AND 19 IN GROUP B

	Ad Lib T_c	Activity	Restricted T_c	Activity
Light period	37.5 ± 0.1	402 ± 25	37.0 ± 0.1	418 ± 65
Dark period	38.3 ± 0.1	1077 ± 107	37.8 ± 0.1	752 ± 61

Nutrition: $F(1, 44) = 41.38$, $p < 0.0001$ and $F(1, 44) = 4.731$, $p < 0.05$.

Nycthemeral: $F(1, 44) = 82.802$, $p < 0.0001$ and $F(1, 44) = 50.411$, $p < 0.0001$.

Nut × Nycto: NS and $F(1, 44) = 5.744$, $p < 0.05$.

trainment to preceding as well as new lighting, and finally a predominant entrainment to new lighting and some double entrainment. Possibly related to this observation is an earlier report (19) of the splitting of temperature and activity rhythms in a small number of male hamsters transferred to constant lighting. In both our and Pickard et al. experiments, the appearance of double rhythms was precipitated by a change in entraining properties of light. Both experiments support the conclusions of others (5) that in the hamster more than one oscillator can control T_c and activity rhythms.

Because we found that light rather than the anticipation of feeding remained the zeitgeber of T_c and activity rhythms in food-restricted hamsters, and that light switch induced doubling of both rhythms in ad lib-fed and in food-restricted hamsters, the proposition that changes in anticipatory activity levels were the cause of changes in T_c could not account for any phenomena we report in this experiment. Nevertheless, we found it of interest to compare the temporal relationship between these two rhythms in food-restricted as well as ad lib-fed hamsters. In this study, T_c and activity rhythms maintained the same phase relationships both before and after the 12-h shift in lighting. Comparison of the rate at which the two rhythms shifted from the entrainment to the original lighting, through the stage of double rhythm frequency, to the entrainment to the shifted lighting, suggests that the T_c rhythm changed earlier than the activity rhythm. And as was discussed earlier in connection with the homeostatic issues in this experiment, T_c (Fig. 3) and general activity (Fig. 5) were correlated at night but not during the day (Table 2). All of this suggests that the timing of both rhythms is under the control of the same oscillator, but that the expression of each rhythm can be modified independently by bioenergetic or other variables.

In conclusion, this study shows that when hamsters lose more than 10% of their body mass, they engage in homeostatic reduction in the levels of their core temperature and of physical activity. These adjustments are carried out within the constraints of nycthemeral temperature and activity rhythms, both of which are firmly entrained to the light stimulus. In addition, when subjected to a 12-h phase shift in lighting, hamsters reveal the operation of two oscillators in the timing of their activity and temperature rhythms.

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