

Daily hoarding opportunity entrains the pacemaker for hamster activity rhythms*

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Summary. The effects on activity rhythms of a daily 30 min opportunity to leave the home cage and hoard seeds from an open field were assessed in Syrian hamsters housed in continuous dim illumination. Six of ten hamsters responded with clear entrainment of their activity rhythms to the hoarding opportunity, as demonstrated by responses to phase shifts and by the onset phase of subsequent freerunning rhythms. No entrainable component separate from the freerunning rhythm was ever observed. Two hamsters showed phase shifts in response to the hoarding opportunity, but they did not meet the criteria for stable entrainment, and two did not respond with noticeable changes in rhythmicity. Ablations of the suprachiasmatic nuclei (SCN) were attempted in three hamsters that had entrained stably to the hoarding time. The effects of partial lesions in two animals indicated that the entrained rhythm was controlled by the light-entrainable pacemaker represented by the SCN. The one animal with an apparently complete lesion, however, developed a clear, but irregular, increase in activity in anticipation of the daily hoarding time. SCN ablation apparently unmasked an oscillator system separate from the SCN and susceptible to entrainment by a non-photic cue. The oscillator mechanism affected by

daily hoarding opportunities in hamsters appears to be tightly coupled to the SCN pacemaker, in contrast to the system in rats that is synchronized by daily feeding schedules.

Introduction

The mammalian circadian system is comprised of a number of circadian oscillators, the best-studied of which is the light-entrainable pacemaker in the suprachiasmatic nuclei (SCN) (Rusak and Zucker 1979; Moore 1983). While the SCN are responsible for the integrity of a large number of circadian rhythms in mammals, there is clear evidence in rodents for the existence of circadian oscillators that survive SCN ablation (Rusak 1977; Stephan et al. 1979; Boulos et al. 1980; Stephan 1981; Terman and Terman 1985). The best-studied example of a circadian system outside the SCN is the mechanism responsible for the ability of rats (*Rattus norvegicus*) to anticipate a limited daily phase of food availability (Bolles and Stokes 1965; Stephan et al. 1979; Boulos and Terman 1980), the physiological substrate for which remains unidentified (Mistlberger and Rechtschaffen 1984; Mistlberger and Rusak 1988).

The output of this food-entrainable oscillator (FEO) is manifest as an activity bout that anticipates the daily time of restricted food availability. Observation of this oscillator's function in rats has generally required either restriction or deprivation of food, but this mechanism can also anticipate the restricted availability of a highly preferred food in free-feeding rats (Mistlberger and Rusak 1987). The activity component entrained by temporally

Abbreviations: SCN suprachiasmatic nuclei; FEO food-entrainable oscillator

* Portions of these results were previously reported at the 1986 meeting of the Animal Behavior Society, Tucson, Arizona, and at the 1987 meeting of the Society for Neuroscience, New Orleans, LA (Rusak et al. 1987)

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restricted feeding can be observed along with the component driven by the SCN pacemaker in intact rats, and it survives SCN ablation (Stephan et al. 1979).

It is not known how general a feature of the mammalian circadian system is a FEO separate from the SCN-based pacemaker. Anticipatory behavior associated with restricted feeding has been observed in rats, squirrel monkeys [*Saimiri sciureus*]; Frim et al. 1984; Aschoff and von Goetz 1986], weasels [*Mustela* spp.; Zielinski 1986], rabbits [*Oryctolagus cuniculus*; Gilge 1987], and the marsupial kowari [*Dasyuroides byrnei*]; O'Reilly et al. 1986]. Little is known, however, about the relations between this activity bout and the SCN in these species.

The circadian system of Syrian hamsters (*Mesocricetus auratus*) has been studied extensively, but it is not known whether hamsters have an anticipatory system analogous to the rat FEO. The methods used to study the FEO of rats cannot readily be applied to hamsters because they do not tolerate the moderate-to-severe temporal restriction on food availability that is required to generate anticipatory activity in rats (Silverman and Zucker 1976). Hamsters may not be capable of consuming large amounts of food opportunistically in a short period of time, and may rely instead on food-hoarding as a mechanism to avoid shortages (Borer et al. 1979; Rowland 1982). Since hamsters are highly motivated to hoard food (Murphy 1971; Lanier et al. 1974), this study was designed to test whether they would show anticipation of a temporally restricted, daily opportunity to hoard.

Several criteria were applied to assess whether any rhythm entrained to the hoarding opportunity reflected a circadian mechanism separate from the SCN pacemaker, and analogous to the rat FEO. The first criterion was the co-existence of a freerunning activity component with an apparently entrained component in constant lighting conditions (cf. Boulos et al. 1980). The second criterion was the initial phase of the freerun emerging after release from apparent entrainment. A freerun could begin from the apparent phase of entrainment or might begin from a different phase set by another oscillator, the output of which is masked by the hoarding opportunity (cf. Boulos and Terman 1980). Finally, SCN ablations were attempted in order to determine whether an apparently entrained component reflected the output of the SCN or of an anatomically distinct mechanism (cf. Stephan et al. 1979).

We found little evidence for a mechanism analogous to the FEO of rats in intact hamsters, and

surprising evidence that a daily hoarding opportunity can entrain the SCN-based, light-entrainable pacemaker in hamsters.

Methods

Apparatus and procedures. Adult male hamsters (LVG: lak, Charles River, Montreal, Quebec) were housed in an apparatus constructed of plexiglas and consisting of a home cage (20 × 40 cm) with an attached tunnel (10 cm in diameter, 93 cm long) leading to a larger open field (47 × 47 cm). Access to the tunnel could be prevented by insertion of a sliding door, which was normally left in place. The room was illuminated continuously by a single red incandescent bulb (Spectro, 10 W) that gave fairly uniform dim illumination (measured using a Model 40 × Opto-Meter, Optikon, Kitchener, Ontario) to all parts of the apparatus (≈0.5–0.6 lux in home cage and open field). There were three similar cages in the room.

Hamsters had free access to water in their home cages and were given sufficient food pellets (Purina) so that they would not run out within 24 h, but were unable to develop a significant hoard. The home cage contained an activity wheel the rotation of which activated a microswitch that was connected to an event recorder and, for the latter part of the study, to an Apple computer that recorded the number of wheel revolutions every 10 min.

Hamsters were housed in constant dim illumination throughout the study. They were first permitted to establish a freerunning rhythm, then were food-deprived for 24 h before their first hoarding opportunity, and before each re-institution of hoarding opportunities. During hoarding availability, a technician entered the room from a darkened outer room daily at a fixed time (1000 Atlantic Standard Time for most animals), placed 15 g of sunflower seeds in the open field, opened the tunnel access door, and left the room. After 30 min, the technician returned, closed the door with the hamster in the home cage, and left one or two food pellets in the home cage. On about half of the hoarding days, the technician had to tap lightly on the home cage to attract the hamster there from the tunnel or open field. When hamsters did not have hoarding opportunities, their cages were not disturbed, although on many of these days the technician entered the room to perform these procedures for other animals.

Hoarding opportunities were continued for several weeks or months, until the freerun had scanned all phase relations to the hoarding time at least once, or until apparently stable entrainment was achieved. In the latter case, the hoarding time was shifted by 6 h in some animals to see if the rhythm followed the phase shift. In most cases of apparent entrainment, hoarding was then discontinued to permit assessment of the phase from which the subsequent freerun originated.

In three animals showing apparent entrainment to the hoarding opportunity, ablations aimed at the SCN were performed. Animals were then retested for entrainment to hoarding opportunities and subsequently released to constant conditions.

Surgery. Hamsters were anesthetized with sodium pentobarbital (80 mg/kg body weight Somnotol; M.T.C. Pharmaceuticals, Mississauga, Ontario), and mounted into a Kopf (Tujunga, CA) stereotaxic frame with the toothbar 2 mm below the interaural line. An electrode made out of a 00 stainless steel insect pin insulated except for 0.4 mm at the tip was aimed stereotaxically at the SCN and bilateral lesions were produced using

a Grass (Quincy, Mass.) radiofrequency lesion maker (LM-4). For two of the hamsters single lesions were produced on each side at 0.5 mm anterior to bregma, 0.3 mm lateral to the midline, and 7.5 mm below dura, by passing current equivalent to approximately 8–10 mA for 15 s at each site. For one animal two such lesions were produced on each side, one pair at 0.5 mm anterior to bregma and one pair at 0.2 mm caudal to bregma.

At the end of the study, ablated animals were killed with a barbiturate overdose. Their brains were perfused, sectioned coronally at 40 μ m and stained with cresyl violet for histological analysis. The anterior SCN was ablated in all three animals. A drawing tube was used to trace sketches of the lesions at middle and caudal levels of the SCN without knowledge of the behavioral results in order to assess the completeness of the lesions.

Results

Six of ten hamsters studied showed apparent entrainment of the previously freerunning activity rhythm during the period of daily hoarding opportunities. The activity rhythms of two hamsters freeran without responding to the hoarding opportunity, except by showing some degree of masking (top of Fig. 1). Hamsters were considered entrained if they expressed an approximately 24-h period with a stable phase relation to the hoarding time (e.g. Fig. 2). In addition, they had to either show a period different from 24 h when they were not hoarding (middle of Fig. 2), or follow a phase shift in the hoarding time (Fig. 3). All animals initially showed freerunning periods greater than 24 h. Entrainment was usually achieved gradually over many weeks, and might not occur until a particular phase relation between activity onset and the hoarding opportunity occurred a second time (Fig. 2).

When apparent entrainment was seen, subsequent freeruns always originated from the phase of entrainment (Figs. 2 and 3), and the period expressed often differed from the 24-h period shown during entrainment (Fig. 2). In other hamsters, freeruns after entrainment expressed periods indistinguishable from 24 h, but the appearance of transients approaching a new steady-state when hoarding opportunities were restored at a new phase provided clear evidence that the rhythms had been entrained, rather than expressing a near 24-h freerun (Fig. 3). Two hamsters showed substantial rhythm disruptions or phase changes in their activity when hoarding was instituted (similar to those seen near the top of Fig. 4), but did not meet our criteria for entrainment.

There was no evidence for entrainment of an oscillator system distinct from that driving the activity rhythm under freerunning conditions; en-

trained and freerunning components were never observed simultaneously. Wheel-running activity onsets either anticipated the hoarding time slightly or followed immediately after the hoarding opportunity. The phase of entrainment was not necessarily consistent during repeated tests in a single animal, and often drifted slightly during a long test (Fig. 3).

Two entrained animals sustained large, but subtotal, lesions of the SCN (Fig. 5, top and middle). One hamster (#2b, Fig. 2) showed a gradual 10-h advance in his activity onset time after the lesion, and then became stably entrained to the hoarding opportunity. He subsequently freeran in constant conditions with a clear circadian rhythm that gradually shortened to less than 24 h. The other hamster with a partial lesion (#3b, Fig. 3) began to freerun with a short period (23.5 h) some weeks after surgery and failed to entrain again. This hamster did show a change in phase and pattern of the freerun when activity onset approached the hoarding time, which might represent relative coordination.

The one hamster with an apparently complete SCN lesion (#1c; Fig. 5, bottom) gradually developed a distinct concentration of activity that anticipated the hoarding opportunity by several hours, but had no sharply defined onset phase (Fig. 4). This hamster differed from those with surviving SCN tissue in that the entrained rhythm was lost immediately when the hoarding opportunity was discontinued. This hamster failed to generate a clear freerunning activity rhythm in constant conditions, although some rhythmic components emerged about two weeks after hoarding opportunities were discontinued.

Hamsters typically ate or retrieved to their home cages most or all of the seeds provided. There was no obvious correlation between regularity of hoarding and entrainment: one hamster which hoarded irregularly or incompletely still entrained (#1c, Fig. 4), and one which hoarded all the seeds regularly failed to entrain (#3c, Fig. 1). The one hamster with a complete SCN lesion (1c) and one with a large, but incomplete, lesion (3b) began to show unusual behaviors after surgery. Hamster 1c frequently and 3b occasionally hoarded seeds to a corner of the open field. Each of these hamsters also occasionally retrieved seeds or food pellets from the home cage and stored them in the open field, and each was occasionally found asleep in the open field after the hoarding time. Other hamsters did not hoard to the open field, nor sleep there, and neither of these animals had done so before surgery.

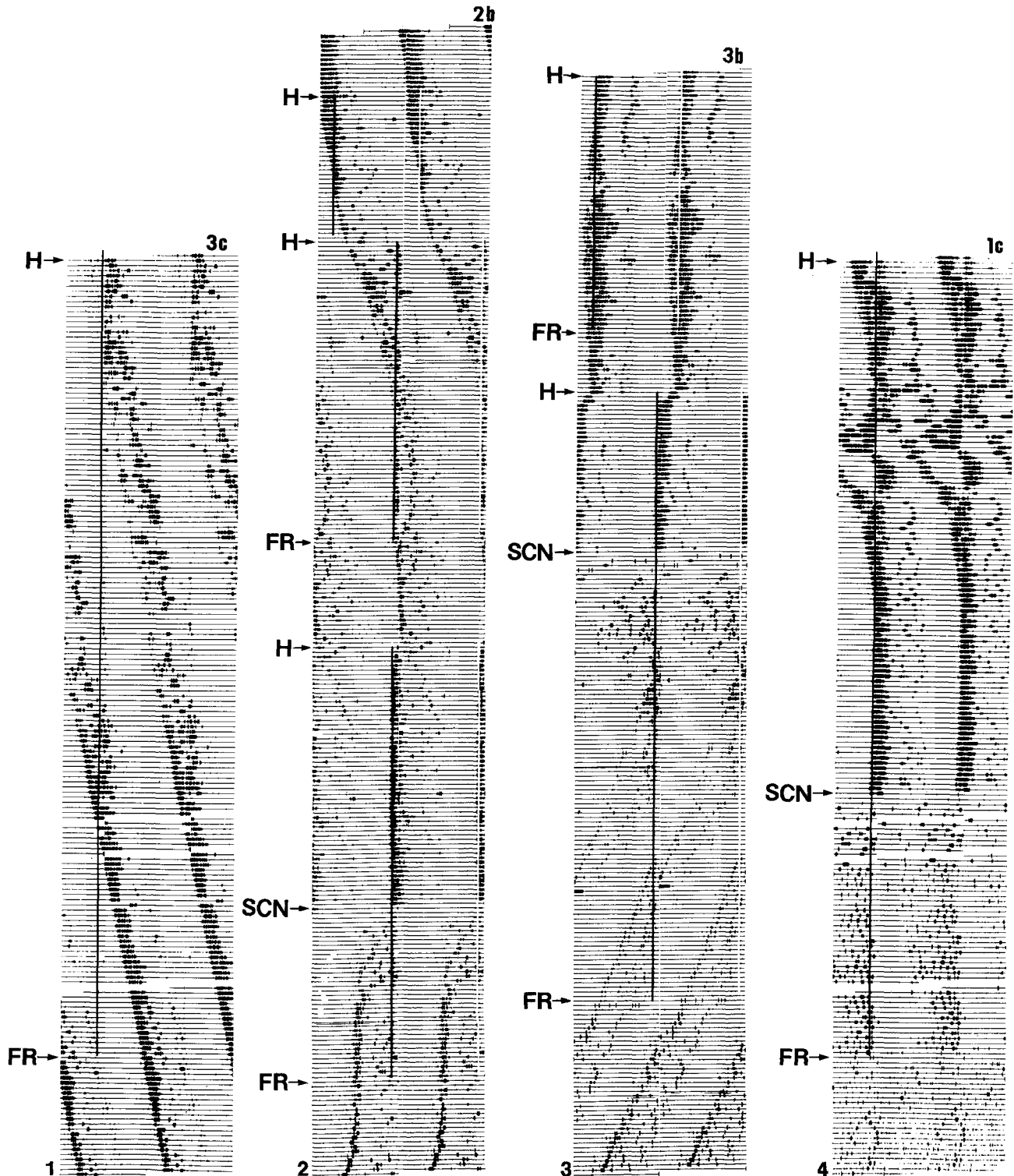


Fig. 1. Computer-generated, actogram-style chart of the wheel-running activity record for hamster 3c while housed in continuous dim red illumination. The height of the black mark for each 10-min bin is proportional to the intensity of activity in that interval. A straight line indicates no activity and blank areas represent missing data. Preceding portions of the record that show the freerun prior to the imposition of the daily hoarding opportunity (*H*) were not recorded by computer and are not shown here. In all cases, hamsters initially freerun with periods greater than 24 h, as illustrated in Fig. 2. The 24-h record is double-plotted, with the vertical line on the left panel indicating the beginning of the daily 30-min hoarding opportunity. At the point marked *FR* the hoarding opportunity was discontinued. This hamster failed to entrain to the hoarding opportunity

Discussion

Although most hamsters appeared to entrain to the hoarding opportunity, it must for several reasons be considered a fairly weak entraining cue compared to a photic stimulus. First, only 6/10 hamsters entrained unambiguously. Second, entrainment did not always occur on the first pass of the rhythm through the hoarding time, and often developed gradually over many weeks as the freerunning period shortened. Third, the phase of entrainment was not always strongly conserved. Finally, one previously entrained rhythm began to freerun when the period shortened to approximately 23.5 h after partial SCN damage, suggesting a fairly narrow entrainment range.

Entrainment effects were apparently exerted on the pacemaker system represented by the SCN, and not on a separate, or separable, oscillator, such as the one affected by feeding cycles in rats. There were no clear instances of co-existing freerunning and food-entrained activity components, although the disrupted rhythms and period changes sometimes seen when hoarding was imposed (e.g., top of Fig. 4) might represent a weak form of this phenomenon. The freerunning rhythm after release from entrainment always originated from the apparent phase of entrainment, and the onsets of entrained rhythms were always continuous with both the prior and subsequent freeruns. The effects of partial SCN ablations in shortening the freerunning period or advancing the entrained phase (cf. Aschoff 1965) are consistent with the known effects of such lesions on the SCN pacemaker (Pickard and Turek 1985). When a partial lesion apparently drove the period of the surviving SCN tissue outside the range of entrainment, no other entrained component emerged.

All of this evidence is consistent with an effect of the hoarding opportunity exclusively on the light-entrainable pacemaker for activity rhythms represented by the SCN. The single case of an apparently complete SCN ablation complicates this

interpretation. One might have predicted an inability to entrain after complete SCN lesions, but this hamster gradually developed a clear, although irregular, rhythm that anticipated the hoarding time. This rhythm did not retain the phase of the prior entrained rhythm, nor did it gradually advance to a new earlier phase relation, as did the activity rhythm of one entrained hamster with a partial lesion (Fig. 2). Instead, initially scattered activity bouts gradually concentrated in the hours preceding the hoarding opportunity.

This behavior parallels the concentration of activity bouts during the dark phase of an imposed lighting cycle observed after SCN ablation in some hamsters (Rusak 1977). This finding has been interpreted as representing the synchronization by an external cue of a surviving population of extra-SCN circadian oscillators that are normally regulated by the SCN pacemaker (Rusak 1982). It is possible that the hoarding opportunity had a similar effect on extra-SCN oscillators in this hamster. Whether these hypothetical oscillators are considered equivalent to the FEO of rats depends on one's hypothesis about the unknown underlying mechanism of the rat FEO. There is certainly no evidence to suggest that the rhythm seen in this one ablated animal has the features of persistence (Coleman et al. 1982), expression of transients (Stephan 1984), a limited range of entrainment (Stephan 1981), and coupling relations to the SCN (Stephan 1986) that characterize the rat FEO. At a minimum, the rat and hamster mechanisms are distinguished by the fact that the extra-SCN oscillators in rats that are affected by restricted feeding are more readily dissociated from the SCN pacemaker and are capable of being expressed behaviorally in its presence.

The cues associated with the hoarding opportunity that are required to produce entrainment are not known. The consistency with which seeds were hoarded did not seem to be correlated with the tendency to entrain, so consumption of the seeds is unlikely to be a critical factor. It may be that

Fig. 2. Activity record of hamster 2b; symbols as in Fig. 1. This hamster entrained to the second imposition of the hoarding opportunity, free-ran when it was discontinued, and re-entrained when it was re-imposed. On the day marked *SCN* the hamster underwent surgery which resulted in a partial ablation of the suprachiasmatic nuclei. It subsequently entrained to the hoarding opportunity with an altered phase relation and freerun under constant conditions

Fig. 3. Activity record of hamster 3b; symbols as in preceding figures. This hamster entrained to each imposition of the hoarding opportunity and showed clear transients during re-entrainment before surgery. It received a partial lesion of the suprachiasmatic nuclei and subsequently freerun with a short period, showing only relative coordination to the hoarding opportunity

Fig. 4. Activity record of hamster 1c; symbols as in preceding figures. This hamster entrained to the hoarding opportunity before surgery and developed an anticipatory rhythm after undergoing complete ablation of the suprachiasmatic nuclei. It failed to generate a circadian rhythm when the hoarding opportunity was discontinued

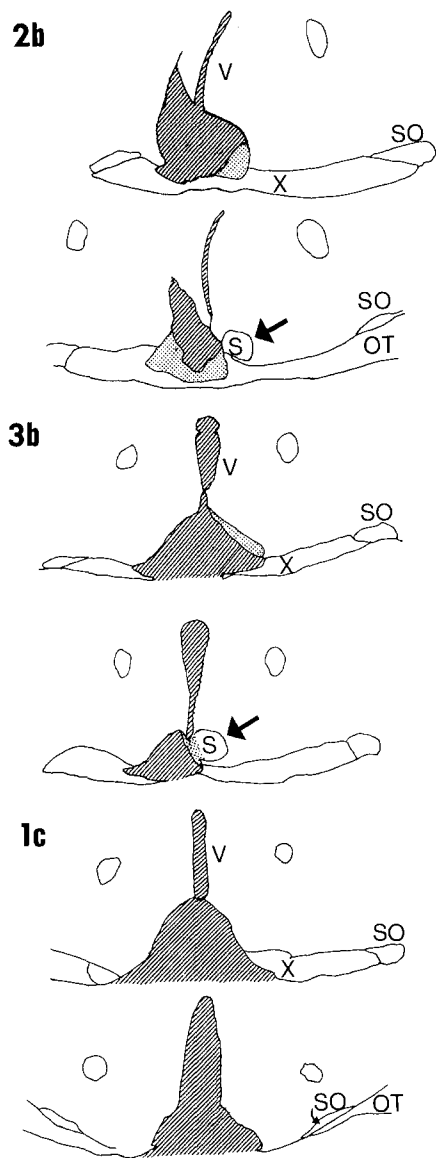


Fig. 5. Lesion reconstructions for the three hamsters whose activity records are shown in Figs. 2, 3 and 4. The two drawings for each animal represent a mid-SCN section (above) and a more caudal section. The arrows and the letter *S* indicate surviving SCN tissue. The hatching indicates the lesion site and the third ventricle (*V*), while the stippling indicates apparent gliosis around the lesion. *X* optic chiasm; *OT* optic tract; *SO* supraoptic nucleus

the critical events were behavioral or motivational consequences of the opportunity to explore or scent-mark the external environment, rather than the opportunity to retrieve seeds to the home cage.

It is doubtful that the activity associated with the hoarding time was alone capable of entraining the pacemaker system. In rats, scheduled opportunities to eat when very hungry generate intense anticipatory activity, but they rarely entrain the

pacemaker (Stephan 1986). Similarly, exposure of hamsters to conspecifics that clearly affects their overt behavior may similarly fail to entrain or modify their SCN-driven activity rhythms (Davis et al. 1987). This contrast should be drawn with caution, however, since these stimuli were not repeated for as many cycles as in this study.

On the other hand, recent reports have described phase-shifts in hamsters resulting from the opportunity to explore a new cage and running wheel, or to interact with another hamster (Mrosovsky and Salmon 1987; Mrosovsky 1987). While these situations include a component of increased activity, it remains to be determined which features of any of these complex situations are necessary for phase-shifting or entrainment of the pacemaker. It is also an open question whether the relevant cues act on the pacemaker directly, as photic information does, or are mediated by effects on an intervening oscillator mechanism which, in turn, influences the pacemaker through their coupling relations.

Whatever the mechanism for the effects of hoarding opportunities, our results demonstrate that cues associated with the performance of a highly motivated behavior can directly or indirectly affect the central pacemaker of the hamster circadian system. These effects contrast sharply to those of food restriction in rats, since the SCN-based pacemaker in rats is rarely affected by feeding schedules, which instead influence a FEO that is expressed independently of the pacemaker. The data from intact hamsters provide little support for the existence of a system strongly analogous to the FEO of rats. Nevertheless, the fact that one hamster sustained an SCN ablation that did not permit generation of a freerunning rhythm, yet still synchronized its activity to the hoarding time suggests that there are also similarities between these systems. The differences may reflect stronger coupling between the SCN pacemaker and extra-SCN oscillators in hamsters than in rats (cf. Aschoff and von Goetz 1986; Stephan 1986). Because of this strong coupling, the extra-SCN oscillators may entrain the SCN when they are affected by non-photic cues, but they can be expressed independently only when the SCN are ablated.

Two hamsters with large lesions of the SCN started to hoard food into the open field and to sleep in that area. Since no control surgeries were attempted it is not certain that this is a specific response to SCN damage. There is, however, related evidence from one hamster tested in an apparatus including a home burrow and open field (Rusak 1975). After sustaining an SCN lesion, that

hamster distributed its activity in short bouts throughout the 24-h day and no longer discriminated between the burrow and open-field in terms of timing of activity. It may be that the SCN play a role in regulating the movements of hamsters between their burrows and the external environment. In its absence, animals may not distribute their behaviors appropriately in either the temporal or spatial domain.

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References

- Aschoff J (1965) The phase-angle difference in circadian periodicity. In: Aschoff J (ed) *Circadian clocks*. North-Holland, Amsterdam, pp 262–276
- Aschoff J, Goetz C von (1986) Effects of feeding cycles on circadian rhythms in squirrel monkeys. *J Biol Rhythms* 1:267–276
- Bolles RC, Stokes LW (1965) Rat's anticipation of diurnal and a-diurnal feeding. *J Comp Physiol Psych* 60:290–294
- Borer KT, Rowland N, Mirow A, Borer RC, Kelch RP (1979) Physiological and behavioral responses to starvation in the golden hamster. *Am J Physiol* 236:E105–E112
- Boulos Z, Terman M (1980) Food availability and biological rhythms. *Neurosci Biobehav Rev* 4:119–131
- Boulos Z, Rosenwasser AM, Terman M (1980) Feeding schedules and the circadian organization of behavior in the rat. *Behav Brain Res* 1:39–65
- Coleman GJ, Harper S, Clarke JD, Armstrong S (1982) Evidence for a separate meal-associated oscillator in the rat. *Physiol Behav* 29:107–115
- Davis FC, Stice S, Menaker M (1987) Activity and reproductive state in the hamster: independent control by social stimuli and a circadian pacemaker. *Physiol Behav* 40:583–590
- Frim DM, Boulos Z, Moore-Ede MC (1984) Restricted but unsignaled daily food availability synchronizes anticipatory behavior but fails to entrain other circadian rhythms in the squirrel monkey. *Soc Neurosci Abstr* 10:504
- Jilge B (1987) Der Circadianrhythmus des Kaninchens im Licht-Dunkelwechsel, in Abwesenheit des Zeitgebers und bei zeitrestriktiver Fütterung. *Dtsch Tierärztl Wochenschr* 94:18–23
- Lanier DL, Estep DQ, Dewsbury DA (1974) Food hoarding in muroid rodents. *Behav Biol* 11:117–187
- Mistlberger RE, Rechtschaffen A (1984) Recovery of anticipatory activity to restricted feeding in rats with ventromedial hypothalamic lesions. *Physiol Behav* 33:227–235
- Mistlberger RE, Rusak B (1987) Palatable daily meals entrain anticipatory activity rhythms in free-feeding rats: dependence on meal size and nutrient content. *Physiol Behav* 41:219–226
- Mistlberger RE, Rusak B (1988) Food anticipatory circadian rhythms in paraventricular and lateral hypothalamic ablated rats. *J Biol Rhythms* 3:277–291
- Moore RY (1983) Organization and function of a central nervous system circadian oscillator: the suprachiasmatic hypothalamic nucleus. *Fed Proc* 42:2783–2789
- Mrosovsky N (1987) Phase response curves for social entrainment. *J Comp Physiol A* 162:35–46
- Mrosovsky N, Salmon PA (1987) A behavioural method for accelerating re-entrainment to new light-dark cycles. *Nature* 330:372–373
- Murphy MR (1971) Natural history of the Syrian golden hamster – A reconnaissance expedition. *Am Zool* 11:632
- O'Reilly H, Armstrong SM, Coleman GJ (1986) Restricted feeding and circadian activity rhythms of a predatory marsupial, *Dasyuroides byrnei*. *Physiol Behav* 38:471–476
- Pickard GE, Turek FW (1985) Effects of partial destruction of the suprachiasmatic nuclei on two circadian parameters: wheel-running activity and short-day induced testicular regression. *J Comp Physiol A* 156:803–815
- Rowland N (1982) Failure by deprived hamsters to increase food intake: some behavioral and physiological determinants. *J Comp Physiol Psychol* 96:591–603
- Rusak B (1975) Neural control of circadian rhythms in behavior of the golden hamster, *Mesocricetus auratus*. Doctoral thesis, University of California, Berkeley
- Rusak B (1977) The role of the suprachiasmatic nuclei in the generation of circadian rhythms in the golden hamster, *Mesocricetus auratus*. *J Comp Physiol* 118:145–164
- Rusak B (1982) Physiological models of the rodent circadian system. In: Aschoff J, Daan S, Groos GA (eds) *Vertebrate circadian systems: structure and function*. Springer, Berlin Heidelberg New York, pp 62–74
- Rusak B, Mistlberger RE, Losier B, Jones CH (1987) Entrainment of the pacemaker for hamster activity rhythms by daily hoarding opportunity. *Soc Neurosci Abstr* 13:423
- Rusak B, Zucker I (1979) Neural regulation of circadian rhythms. *Physiol Rev* 59:449–526
- Silverman HJ, Zucker I (1976) Absence of post-fast food compensation in the golden hamster (*Mesocricetus auratus*). *Physiol Behav* 17:271–285
- Stephan FK (1981) Limits of entrainment to periodic feeding in rats with suprachiasmatic lesions. *J Comp Physiol* 143:401–410
- Stephan FK (1984) Phase shift of circadian rhythms in activity entrained to food access. *Physiol Behav* 32:663–671
- Stephan FK (1986) The role of period and phase in interactions between feeding- and light-entrainable circadian rhythms. *Physiol Behav* 36:151–158
- Stephan FK, Swann JM, Sisk CL (1979) Entrainment of circadian rhythms by feeding schedules in rats with suprachiasmatic lesions. *Behav Neural Biol* 25:545–554
- Terman M, Terman J (1985) A circadian pacemaker for visual sensitivity? *Ann NY Acad Sci* 453:147–161
- Zielinski WJ (1986) Circadian rhythms of small carnivores and the effect of restricted feeding on daily activity. *Physiol Behav* 38:613–620