

## **Arousal by sexual stimuli accelerates the re-entrainment of hamsters to phase advanced light-dark cycles**

**Gerry I. Honrado and N. Mrosovsky**

Department of Psychology, Sidney Smith Hall, University of Toronto, 100 St. George St., Toronto, Canada M5S 1A1

Received November 11, 1988 / Accepted March 2, 1989

**Summary.** The arousal caused by the 3 h presentation of female socio-sexual cues to male hamsters given an 8 h advance of the light-dark cycle caused an acceleration in the rate of re-entrainment to this new light-dark cycle. This accelerating effect was seen most clearly in animals allowed to run in their wheels in response to a nearby female hamster in estrous condition. However, wheel-running was not a necessary condition for enhancement. In one experiment, males with their wheels prevented from rotating also showed an accelerated rate of re-entrainment; in another experiment, the effect was almost significant ( $P=0.058$ ). Mating itself seemed to counteract this accelerating effect. Males aroused by nearby but inaccessible estrous females re-entrained quicker than males allowed to mate with an estrous female. Lastly, male hamsters placed in a novel wheel but not allowed to run showed a variable rate of re-entrainment to an 8 h light-dark cycle advance; individuals judged to be sleeping during most of the 3 h in the novel wheel took longer to re-entrain than those judged to be awake during most of the 3 h. These results suggest that there is a general arousal mechanism through which non-specific, non-photic events can enhance the phase advancing actions of a light-entrainable clock.

---

### **Introduction**

Investigations of entrainment of circadian rhythms have concentrated on the role of light-dark cycles. However, it has also become apparent that a number of non-photic stimuli can entrain otherwise free-running rhythms. These stimuli include

temperature (Lindberg and Hayden 1974; Tokura and Aschoff 1983), playback of conspecific song and other auditory stimuli in birds (Gwinner 1966; Menaker and Eskin 1966; Lohmann and Enright 1967), periodic cage changing (Mrosovsky 1988), social interactions (Marimuthu et al. 1981; Honrado 1987; Mrosovsky 1988; see Regal and Connolly 1980 for review) and induced wheel-running activity (Reebs and Mrosovsky 1989). In addition, periodic feeding can entrain a component of the activity rhythm (Boulos and Terman 1980; Stephan 1984).

Functionally speaking, it seems reasonable that a variety of periodically repeated events relating to food supplies, territory, predators, conspecifics, and temperature would have effects on the programming of behavior over the course of the day. However, in terms of mechanism, it does not seem necessary to postulate separate oscillators for different non-photic events. It is more plausible that various non-photic events exert their effects through some common arousal oscillator, or that arousal, in whatever way it is produced, modifies the operation of the light-entrainable oscillator(s) (Honrado 1987; Mrosovsky 1988).

If this view is correct, then a variety of arousing, non-photic events should have fairly similar effects on circadian rhythms. In this paper, we report experiments on the effects of arousal by sexual cues on the circadian activity rhythm of male hamsters. When male hamsters encounter a female hamster in heat, they become very active. Surprisingly, a recent study by Davis et al. (1987) failed to show a synchronizing influence of a continuously nearby female hamster on the free-running activity rhythm of the male, although the latter did become more active on days when the former was in estrus. Similarly, Aschoff and von Goetz

(1988) found that the activity rhythm of blinded male hamsters were not entrained by the daily presentation of females. However, the females stimulated activity in the males and produced a masking effect. In the present experiment, male hamsters were only exposed to females actually in estrous condition; this should be the most arousing socio-sexual stimulus.

Arousal is not a well defined term, operationally or otherwise. When a sleeping male hamster is presented with a female that is in heat, it receives not only specific sexual cues but it is also woken up, is more active, and is probably in a different physiological state than when awake on its own. To investigate the matter of non-specificity of non-photic effects on the circadian system, a number of additional experiments were run. In some cases hamsters were prevented from mating. In this situation, males are generally very active, running vigorously if wheels are available; the amount of activity was manipulated by preventing the running wheels from rotating. In other cases, mating was allowed. It is known that after bouts of mating, there is a refractory period during which the male is relatively inactive. Finally, in one experiment without any females present at all, we investigated the effects of being awake (but without the opportunity to run in a wheel) on the state of the activity rhythm.

In all these experiments, the testing method chosen to investigate the effects of non-photic stimuli was to combine them with an advance in the light-dark cycle and then measure how much the rate of re-entrainment was accelerated. This method has several advantages. Because the light-dark cycles are always present, rhythm anomalies associated with continuous light and decreasing activity associated with continuous dark are avoided. Onset of activity remains clearly defined. Because the non-photic stimuli occur only on occasional days when the light-dark cycle is shifted, rather than repeatedly, habituation is avoided. Finally, the effects seen in this method are consistent with those seen with other testing methods. For instance, phase response curves for non-photic stimuli presented in constant conditions predict that these stimuli should accelerate entrainment when given 6 h before the onset of activity during adjustment to advanced light-dark cycles, and indeed this is what has been found (Turek and Losec-Olson 1986; Van Reeth and Turek 1987; Mrosovsky 1988; Reeb and Mrosovsky 1989; Mrosovsky and Salmon 1987). For the present work, the phase shift method was not only easier to quantify, it was also more convenient.

## Methods

### *Subjects and housing conditions*

Golden hamsters *Mesocricetus auratus* [Hsd:(SYR) BR], aged 6–7 weeks, were purchased from Harlan Sprague-Dawley Inc. (Indianapolis) for use in Experiments I and II. The male hamsters used in Experiment III, 20 weeks old at the time of testing, were obtained from Charles River, Montreal (LAK:LVG).

The males were housed individually in solid walled metal cages (36 × 20 × 30 cm, L × W × H) containing an activity wheel (17.5 cm diameter). The females were kept in a different room and also housed in individual cages (37 × 22 × 19 cm, L × W × H), with no access to running wheels. Laboratory Rodent Chow (Purina #5001) and water were available *ad libitum*.

Room temperatures for the different rooms were maintained at approximately 20° ± 2° C. Light intensity during the day portion of the light cycles used in the male rooms was about 100 lux (measured by Gossen light meters).

### *Experimental design*

Experimental and control tests for the effects of female hamsters in estrous condition were run sequentially. We were unable to test control animals not presented with females at the same time because odor cues from females with the experimental animals were liable to permeate the whole room. The sequential design used instead had the added advantage of controlling for individual differences in the rate of phase shifting; individuals were tested first with the experimental manipulation and control tests on the same individuals took place subsequently.

### *Arousal by socio-sexual cues*

*Shift 1: Socio-sexual cues.* Upon arrival, the females were put in a separate room, in another part of the building from the males. Vaginal smears were taken daily. Nineteen males were placed in their cages and their running wheel activities monitored on an Esterline Angus event recorder. All animals were placed under a 14:10 LD cycle. For the females, dark onset occurred at 1600 h; they were kept on this cycle throughout the course of the project. For the males, dark onset occurred at 0200 h for the first 17 days. On day 18, starting with an advance of the dark onset, their light cycle was advanced by 8 h so that dark onset was now at 1800 h.

The males were divided into 3 groups:

**Group 1.** One hour after the new dark onset (ie., 1900 h, or about 7 h before the previous onset of activity) estrous females were introduced into the cages of 9 males. To prevent fighting and mating, the female was enclosed in a small restraining cage (19.5 × 8 × 11 cm, L × W × H) suspended at one end of the male's cage. After 3 h the females were removed. Wheels were free to turn.

**Group 2.** Six other males in the same room were similarly exposed to estrous females in the restraining cages. However, for this group, the running wheels were prevented from rotating by wiring them to the cage cover. Three hours later the females were removed. The wheels remained blocked until 0100 h, about 1 h before the previous activity onset.

**Group 3.** This group consisted of 4 other males in the same room. They were not directly exposed to females, but presumably received olfactory and auditory cues from the estrous females introduced into the cages of the males in the other groups.

*Shift 2: First control manipulation.* Twenty-seven days after the first phase shift, all the males were given a second 8-h phase advance of the light-dark cycle so that now dark onset was at 1000 h. One hour after the new dark onset (1100 h), a clean, empty restraining cage was placed into each male's home cage. Three hours later, the restraining cage was removed.

*Shift 3: Second control manipulation.* After another 27 days, a third phase advance took place; dark onset now occurred at 0200 h once again. The room was not entered at the time of the dark onset; the timer was adjusted previously with minimal disturbance to the animals.

### *Mating*

The aim of this experiment was to discover whether actual mating was capable of accelerating the rate of re-entrainment to a light cycle advance. The same hamsters from Experiment I, now 18–19 weeks old, were used. Again, the males were exposed to an 8-h phase advance of the light-dark cycle, starting with a new dark onset at 1800 h. The animals were divided into two groups:

**Mated group:** One hour after the new onset of darkness (1900 h), estrous female hamsters were introduced into the cages of 8 males. After a 1-h interaction, the females were removed. The males' wheels were prevented from rotating for 6 h, ie., until 0100 h, 1 h before the former dark onset.

**Non-mated group:** Just as in the mated group, these animals had an estrous female nearby but they were not allowed to mate. The females were held within small restraining cages. Additionally, the males' wheels were blocked. In other words, this group was similar to group 2 of Experiment I except that here the females were available for only 1 h.

The data on the rate of re-entrainment for these 2 groups were compared with those shown by the same individuals when previously given an 8-h advance in the light-dark cycle but no additional stimulation (Experiment I, Shift 3).

### *Wakefulness*

The aim of this experiment was to assess the influence of being awake, but without wheel running, on the rate of re-entrainment. Nineteen male hamsters (LAK:LVG) were used. These animals had previously been given a number of phase advances as described in Mrosovsky and Salmon (1987). The present experiment took place 25 days after the last phase shift described previously. The hamsters were divided into three groups:

**Group 1:** Six males were confined to novel running wheels for 3 h on the same day they were given an 8-h phase advance. The period in the novel wheels started 1 h after the advanced onset of darkness (see Mrosovsky and Salmon 1987 for details).

**Group 2:** Seven males were moved into the novel wheels at the same time and for the same duration as group 1. However, for these animals, the wheels were prevented from turning. The behavior of these animals was briefly and quietly observed using an infrared nightscope viewer at 1-h intervals during the time they were in the novel wheels. If the animals were curled up and immobile, they were scored as being asleep (score = 1); if they were sitting or moving with their eyes open they were scored as being awake (score = 0). Sleep scores (possible range 0–3) were obtained by combining data from 3 observation times, ie., a score of 3 meant an animal was observed to be sleeping at all 3 observation times.

**Group 3:** The remaining 6 animals were left undisturbed in their home cage on the day of the phase shift.

### *Data analysis*

For each experiment, the dependent variable measured was the number of days it took the animal to re-entrain to each new 8-h light cycle phase shift. The criterion for re-entrainment was that activity

onset had to occur within 30 min of the time of the new dark onset (Van Reeth and Turek 1987; Mrosovsky and Salmon 1987). Activity onset was defined as 5 min of continuous wheel running followed by at least another continuous 5-min burst of running within the next 30 min (Lees et al. 1983).

Analyses of variance were performed on data from Experiments I and III. One-tailed, paired comparison *t*-tests were used to analyze data from Experiments I and II.

To ensure that the effects obtained were not due to differences in pre-shift phase angles for the three groups, a 3 × 3 (group × shift) ANOVA was performed on the average onset time for the 5 days preceding each of the three phase shifts in the light cycle. There was no significant group effect ( $P > 0.315$ ) and no significant interaction effect ( $P > 0.194$ ). The shift effect was significant ( $P < 0.001$ ) as expected since each new light cycle was 8 h phase advanced from the previous one.

## Results

### Arousal effects

Phase shifting occurred considerably faster when estrous female hamsters were introduced into the room than on the two subsequent occasions when they were absent (Fig. 1; see Fig. 2 for individual records). The shift effect (shift 1 vs shift 2 vs shift 3) was highly significant (3 × 3, mixed design ANOVA;  $F(2,32) = 15.17$ ,  $P < 0.001$ ). Other experiments with an 8-h advance of the LD cycle have shown that earlier activity onsets following nonphotic events do indeed represent the position of the pacemaker: if hamsters are placed in continuous darkness one day after a nonphotically accelerated phase shift, their free-running rhythms take off from a time near the advanced activity onsets rather than from near their pre-shift activity onsets (Mrosovsky, in press).

There was no significant difference between the two control manipulations, i.e., placing an empty restraining cage into the male's cage did not accelerate phase shifting when compared to not entering the room at all (2 × 3, mixed design ANOVA using only shift 2 and shift 3 data;  $F(1,15) = 0.11$ ,  $P = 0.746$ ). Although on average introducing the restraining cage did not have an effect, a few animals did entrain rapidly. Perhaps placing a different object in their cage caused some disturbance.

The results establish that socio-sexual stimuli occurring during a few hours before normal activity onset, when coupled with a phase advanced

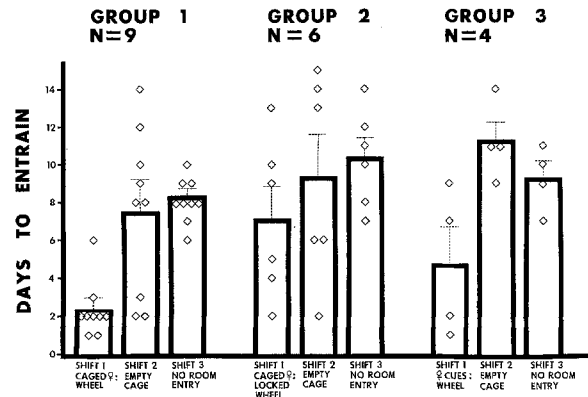


Fig. 1. Mean number of days to re-entrain ( $\pm$  SEM) to three, 8-h phase advances of the light-dark cycle for each of three different groups of animals. Each group was given a different type of socio-sexual arousal on the day of the first light shift. For the second 8-h light-dark cycle advance, a small restraining cage was placed into the males' cages for 3 h. The third shift consisted of advancing the light-dark cycle with minimum disturbance to the animals

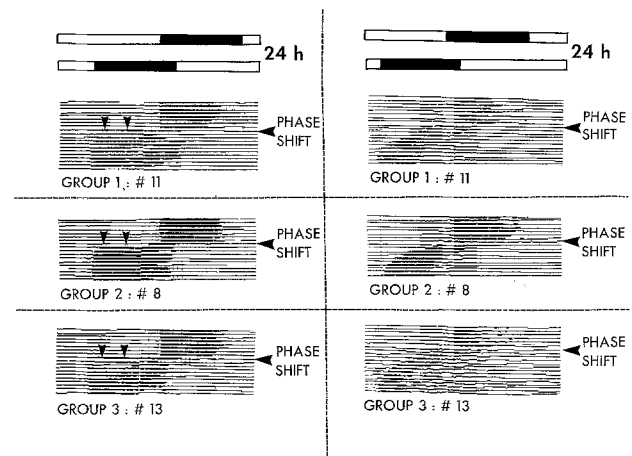


Fig. 2. Activity records for typical animals from the three experimental groups in Experiment I. The records on the left show shift 1, during which the animals were exposed to socio-sexual cues for 3 h (downward pointing arrows). The records on the right show shift 3, a control manipulation, for the same individual animals. Each line shows 24 h, with each day mounted below the previous day. Black marks indicate wheel-running. Open and solid horizontal bars depict the light-dark cycles prevailing before and after the 8-h phase shift

light-dark cycle, accelerate re-entrainment to this new light-dark cycle. However, it is not simply being exposed to estrous females that produces this effect; how the animal behaves in this situation is also important. The rate of re-entrainment was faster when an animal could run in its wheel (3 × 3 ANOVA, significant group effect:  $F(2,16) = 3.81$ ,  $P < 0.05$ ; 1-way ANOVA for shift 1 data only:  $F(2,16) = 4.54$ ,  $P < 0.028$ ). In fact, the latter analy-

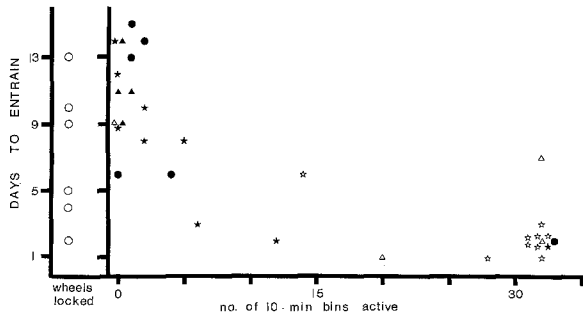


Fig. 3. The relationship between the number of days it took to re-entrain to phase shifts 1 and 3, and the amount of activity exhibited by the animals during those shifts. Open figures are shift 1 animals; closed figures are shift 3 animals. Stars are group 1 animals; circles are group 2 animals and; triangles are group 3 animals

sis showed that having an estrous female and a wheel to run in was most conducive to accelerated re-entrainment; having a female but no wheel to run in was the least conducive.

The importance of being able to run in the wheel while being aroused by an estrous female can be illustrated in another way. The number of 10-min bins in which animals registered wheel running over the 6-h period starting from the introduction of the non-photic manipulations (i.e., starting 1 h after the advanced onset of darkness) was scored for all tests where an animal had access to a rotating wheel (i.e., excluding group 2, shift 1). Data from shift 3, when the room was not entered, were also excluded, because there was virtually no running exhibited by any of the animals. The activity scores were negatively correlated with the number of days taken to re-entrain ( $r = -0.82$ , adjusted  $R$ -square = 0.66). A regression ANOVA yielded a very significant correlation ( $F(1,30) = 60.08$ ;  $P < 0.00001$ ; see Fig. 3).

Nevertheless, even with a locked wheel, there was some enhancement of phase shifting with a female present. In Experiment I, the difference between the rate of re-entrainment on shift 1 versus shift 3 for the group 2 animals fell just short of significance (paired  $t$ -test;  $t(5) = 1.93$ ,  $P = 0.058$ ; see Fig. 2, group 2). In Experiment II, the non-mated control animals showed a significantly accelerated rate of re-entrainment [paired  $t$ -test;  $t(4) = 2.80$ ,  $P < 0.025$ ].

#### Mating effects

Mated animals did not shift faster than they had when tested previously without any change other than that in the LD cycle, i.e., without any non-photic input [paired  $t$ -test;  $t(7) = 0.45$ ,  $P = 0.34$ ].

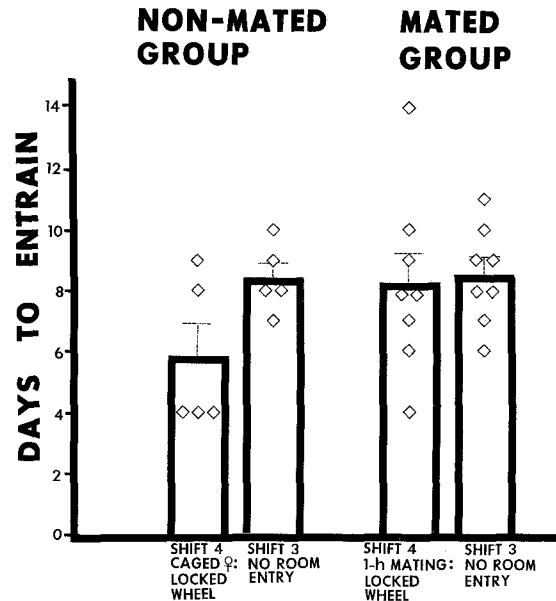


Fig. 4. Mean number of days ( $\pm$ SEM) to re-entrain to two, 8-h phase advances of the light-dark cycle. Shift 3 is the control manipulation; shift 4 consists of either mating the males with estrous females or arousing them with cage-restrained estrous females

However, as already mentioned, the non-mated males exposed to an estrous female within a restraining cage did shift faster than they had when merely given a phase shift in the light cycle [ $t(4) = 2.80$ ,  $P < 0.025$ ], even though their wheels were blocked for 6 h (see Fig. 4).

All mated females became pregnant. At the end of the 1-h interaction period, when the females were removed, some of the mated pairs were fighting.

#### Wakefulness effects

Animals placed in novel wheels shifted much faster (mean: 1.3 days; range: 1–2 days) than those left undisturbed in their home cages (mean: 10.3 days; range: 6–17 days). This confirms previous results (Mrosovsky and Salmon 1987). The rate of re-entrainment of animals moved to novel wheels that were prevented from rotating was highly variable (range: 1–17 days). However, animals with the lowest sleep scores re-entrained rapidly (1–3 days) while those with the higher sleep scores took much longer to re-entrain their activity rhythm (12–17 days). The number of days it took to re-entrain was positively correlated with the sleep score ( $r = 0.81$ , regression ANOVA:  $F(1,5) = 9.44$ ,  $P < 0.026$ ).

## Discussion

Socio-sexual cues from female hamsters greatly accelerate re-entrainment of males exposed to advanced light-dark cycles. These cues need be no more than the smell, and perhaps the sound, of an estrous female, or both. Males left alone in their home cages at the time females were put into the cages of other animals in the room also re-entrained much faster than they did without a non-photic enhancer (Fig. 2, group 3). Extreme care was taken to exclude any light at the time the estrous females were brought into and later removed from the room; thus, the effects were definitely nonphotic. Moreover, had any light been present at the time, the phase response curve for light pulses in constant dark would have predicted a delay or no shift at all (Daan and Pittendrigh 1976; Ellis et al. 1982) instead of the advances seen here.

The rapid phase shift is not only dependent on what stimuli the hamsters receive, but also on how they are able to react to these stimuli. Several pieces of evidence show that the accessibility and use of a running wheel is very important (cf. Yamada et al. 1988). First, when the wheels are blocked, the enhancing effect of the estrous female is diminished (Fig. 1, Group 2 vs Group 1). Second, the rate of re-entrainment correlates strongly with the amount of time spent wheel running (Fig. 3). Possibly, failure to obtain entrainment by social stimuli (Aschoff and von Goetz 1988; Davis et al. 1987) may be accounted for by inadequate durations of induced activity.

While wheel running is a good predictor of fast shifting, such activity is not essential for there to be some enhancing effect. Animals with blocked wheels shifted slightly faster when estrous females were in the room than when there were no non-photic stimuli; one animal in this group adjusted to the new light-dark cycle in 2 days. In the third experiment, where no females were present, simply being in a novel wheel, even though it was locked, produced rapid re-entrainment in those hamsters that kept active rather than curled up. In the present experiments with the estrous females, we did not observe the animals during the 3-h period lest our presence introduce confounding stimuli. Presumably, when an animal re-entrains rapidly without wheel running, it is because it is active outside its wheel.

In considering the importance of running activity, a more interesting case is that of an animal that runs but does not phase shift especially rapidly. The clearest example of this in the present experiment comes from an animal in group 3 (open

triangle on right of Fig. 3). This animal took 7 days to re-entrain whereas other animals that ran just as long took only 1–3 days. Because of this animal and similar though less extreme cases, it would not be justified to say that running activity necessarily produces rapid re-entrainment.

Thus, while wheel running and fast phase shifting are clearly correlated in these experiments, it is possible that rapid re-entrainment results not from wheel running itself, but from something that is often, but not invariably, associated with wheel running. This state can also be associated with activity outside the wheel, but is usually less pronounced in these circumstances.

Whatever the critical factor or factors associated with these enhancers of phase shifting may be, they are probably relatively non-specific. Non-photic enhancement has been produced by triazolam injections (Van Reeth and Turek 1987); with the doses used in hamsters, this benzodiazepine often produces prolonged activity bouts. Non-photic enhancement has also been seen after periods in novel cages (Mrosovsky and Salmon 1987) and with socio-sexual cues in the present experiments. Additionally, single presentations of various non-photic stimuli given about 6 h before the activity onset of free-running animals result in phase advances. In hamsters, this effect occurs with cage-changing, social interactions between pairs of males (Mrosovsky 1988), induced wheel running in novel wheels (Reebs and Mrosovsky 1989), and triazolam (Turek and Losee-Olson 1986). In sparrows, diurnal animals, both playback of conspecific song and a non-conspecific sound have phase advancing effects (Reebs 1989). Since the enhancement of rate of re-entrainment is consistent with an advance portion of the phase response curve in the middle of the normal inactive phase of the cycle, these various manipulations might all involve a common non-specific factor, possibly some form of arousal.

Whatever this state is, for hamsters, mating itself is not sufficient to produce it. In Experiment II, wheel running was prevented for 6 h, virtually the whole time until activity onset would normally have occurred under the previous light cycle. However, since other hamsters with their wheels locked for a similar time, but not allowed to mate with an estrous female, did show some enhancement of re-entrainment rate, it may be inferred that something about the mating experience of hamsters may be counteracting the phase advancing effect of the female within a small restraining cage. This counteracting process may be related to the refractory period. To impregnate a female, a male

hamster has to intromit and ejaculate a certain number of times, which takes approximately 20 to 30 min (Bunnell et al. 1977; Huck et al. 1986; Honrado, unpublished), after which the male usually becomes unsollicitous of the same female (Bunnell et al. 1977). It is not suggested that mating itself is not arousing but that the arousal induced by mating may not last long enough. It is clear from Fig. 3 that activity has to persist for 1 to 2 h to produce rapid phase shifts. Often after mating, the male ignores the female or falls asleep. The male's sexual interest can only be renewed with the passage of time or by the presentation of a novel estrous female (Coolidge Effect). Additionally, female receptive and proceptive behaviors decline after mating (Steel 1979). It remains possible that mating would have effects on rate of re-entrainment if presented at a different phase of the cycle, or in a phase delay test. These aspects of non-photic stimuli have not been given as much attention as the phase advancing effect.

The non-specificity of socio-sexual cues in hamsters, or of conspecific song in birds, does not detract from the possibility that non-photic stimuli may play a role in the organization of circadian activity. Non-specific mediation would permit a variety of events, including arousal by sexual stimuli, to modify the timing of an animal's behavior.

*Acknowledgements.* We thank John Glover, Ed Knapp, Philip PeBenito, Ian Spence and especially Peggy Salmon for invaluable assistance. This work was supported by the Natural Sciences and Engineering Research Council of Canada and by University of Toronto Open Fellowships.

## References

- Aschoff J, von Goetz C (1988) Masking of circadian activity rhythms in male golden hamsters by the presence of females. *Behav Ecol Sociobiol* 22:409–412
- Boulos Z, Terman M (1980) Food availability and daily biological rhythms. *Neurosci Biobehav Rev* 4:119–131
- Bunnell BN, Boland BD, Dewsbury DA (1977) Copulatory behavior of golden hamsters (*Mesocricetus auratus*). *Behav* 61:180–205
- Daan S, Pittendrigh CS (1976) A functional analysis of circadian pacemakers in nocturnal rodents. III. Heavy water and constant light: homeostasis or frequency? *J Comp Physiol* 106:253–266
- 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
- Ellis GB, McKIveen RE, Turek FW (1982) Dark pulses affect the circadian rhythm of activity in hamsters kept in constant light. *Am J Physiol* 242:R44–R50
- Gwinner E (1966) Periodicity of a circadian rhythm in birds by species-specific song cycles (Aves, Fringillidae: *Carduelis spinus*, *Serinus serinus*). *Experientia* 22:765–766
- Honrado GI (1987) The effects of sociosexual cues on the light-entrained and free-running circadian activity rhythms of male golden hamsters, *Mesocricetus auratus*. M. Sc. Thesis, Department of Zoology, University of Toronto
- Huck UW, Lisk RD, Thierjung C (1986) Stimulus requirements for pregnancy initiation in the golden hamster (*Mesocricetus auratus*) change with time of mating during the receptive period. *J Reprod Fert* 776:449–458
- Lees JG, Hallonquist JD, Mrosovsky N (1983) Differential effects of dark pulses on the two components of split circadian activity rhythms in golden hamsters. *J Comp Physiol* 153:123–132
- Lindberg RG, Hayden P (1974) Thermoperiodic entrainment of arousal from torpor in the little pocket mouse, *Perognathus longimembris*. *Chronobiologia* 1:356–361
- Lohmann M, Enright JT (1967) The influence of mechanical noise on the activity rhythms of finches. *Comp Biochem Physiol* 22:289–296
- Marimuthu G, Rajan S, Chandrashekar MK (1981) Social entrainment of the circadian rhythm in the flight activity of the microchiropteran bat *Hipposideros speoris*. *Behav Ecol Sociobiol* 8:147–150
- Menaker M, Eskin A (1966) Entrainment of circadian rhythms by sound in *Passer domesticus*. *Science* 154:1579–1581
- Mrosovsky N (1988) Phase response curves for social entrainment. *J Comp Physiol A* 162:35–46
- Mrosovsky N (in press) Non-photic enhancement of adjustment to new light-dark cycles: masking interpretation discounted. *J Biol Rhythms*
- Mrosovsky N, Salmon P (1987) A behavioural method for accelerating re-entrainment of rhythms to new light-dark cycles. *Nature* 330:372–373
- Reebs SG (1989) Acoustical entrainment of circadian activity rhythms in house sparrows: constant light is not necessary. *Ethology* 80:172–181
- Reebs SG, Mrosovsky N (1989) Effects of induced wheel running on the circadian activity rhythms of syrian hamsters: entrainment and phase response curve. *J Biol Rhythms* 4:39–48
- Regal PJ, Connolly MS (1980) Social influences on biological rhythms. *Behav* 72:171–199
- Steel E (1979) Short-term, postcopulatory changes in receptive and proceptive behavior in the female syrian hamster (*Mesocricetus auratus*). *Horm Behav* 12:280–292
- Stephan FK (1984) Phase shifts of circadian rhythms in activity entrained to food access. *Physiol Behav* 32:663–671
- Tokura H, Aschoff J (1983) Effects of temperature on the circadian rhythms of pig-tailed macaques, *Macaca nemestrina*. *Am J Physiol* 245:R800–R804
- Turek FW, Losee-Olson S (1986) A benzodiazepine used in the treatment of insomnia phase-shifts the mammalian circadian clock. *Nature* 321:167–168
- Van Reeth O, Turek FW (1987) Adaptation of circadian rhythmicity to shift in light-dark cycle accelerated by a benzodiazepine. *Am J Physiol* 253:R204–R207
- Yamada N, Shimoda K, Ohi K, Takahashi S, Takahashi K (1988) Free-access to a running wheel shortens the period of free-running rhythm in blinded rats. *Physiol Behav* 42:87–91