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# Sex Differences and Effects of Social Cues on Daily Rhythms Following Phase Advances in *Octodon degus*

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GOEL, N. AND T. M. LEE. *Sex differences and effects of social cues on daily rhythms following phase advances in Octodon degus*. *PHYSIOL BEHAV* 58(2) 205–213, 1995.—Two experiments were designed to determine whether social cues could enhance the rate of resynchronization in body temperature and general activity rhythms in male or female *Octodon degus* following a 6 h phase advance. The first experiment examined average resynchronization rates for animals in each condition. The second experiment examined resynchronization rates for a smaller group of animals, each treated as its own control. Female phase-shifters resynchronized temperature and activity rhythms significantly faster when housed with an entrained (donor) female than those females housed with another phase-shifting female or housed alone. Females housed with entrained males resynchronized their temperature rhythms significantly slower than females housed with entrained females. No differences in resynchronization rate for phase-shifting males existed between test conditions. However, activity rhythms of male controls (housed alone) reentrained significantly faster than those of female controls. These experiments demonstrate a sex difference in (i) reentrainment rate by photic cues alone; (ii) donors' effect on female phase-shifters' resynchronization; and (iii) phase-shifters' resynchronization response to donor cues. In these studies, resynchronization in the presence of another animal could either have been achieved by entrainment of the pacemaker or by masking of the circadian rhythms.

Sex difference    Social cues    *Octodon degus*    Diurnal

A MAJORITY of studies examining the entrainment of circadian rhythms have concentrated on the role of geophysical factors, such as light intensity or ambient temperature, as entrainers or zeitgebers (21). However, other factors, such as social cues, are also capable of acting as nonphotic zeitgebers in free-running animals (24). Thus far, the interaction of photic and nonphotic zeitgebers has received little attention.

Entraining social cues have been demonstrated in several species. Exposure to cycles of the presence/absence of conspecifics (hamsters [*Mesocricetus auratus*], (22); bats [*Hipposideros speoris*], (18); mice [*Mus booduga*], (27)), as well as to daily playbacks of conspecifics' vocalizations at fixed times of day in birds (siskins [*Carduelis spinus*], serins [*Serinus serinus*], (11); house sparrows [*Passer domesticus*], (19,23)), resulted in entrainment of animals in the absence of photic cues. Social entrainment has also been demonstrated by individuals synchronizing their free-running rhythms to each other (deer mice [*Peromyscus maniculatus*], (3); killifish [*Fundulus heteroclitus*], (12); hamsters [*Mesocricetus auratus*], (6); Wistar rats, (26)).

Social entrainment has been hypothesized to be effective in humans (1,29), but the results of these studies are somewhat inconclusive. Aschoff (1) and Wever (29) demonstrated that mem-

bers of a group maintained in isolation produced a common free-running period. However, the controls in these experiments were not ideal: the subjects had control over their own lighting schedule, and it is possible that the reported effects were due to a dominant person(s) controlling the lights, thereby entraining the rest of the group.

Klein and Wegmann (16) examined the effects of social zeitgebers in humans following transmeridian travel. They reported that the shift rate of individuals depended upon their activities, measured by the amount of social contact, for the eight days following flight. The rate of reentrainment was twice as fast when individuals were permitted to leave their rooms every second day as opposed to when they were isolated in their hotel rooms. However, when subjects were allowed to leave their rooms, they were also exposed to sunlight. Thus, the reported effects could quite possibly be attributed to photic rather than social entrainment.

Nearly all previous social entrainment research, except for phase-shifting humans, has been done with animals placed in constant conditions (constant light [LL] or constant darkness [DD]). These studies were important for testing the possibility of social cues as zeitgebers (3,11,12,18,19,23,27), assessing how social cues affect the phase and period of the circadian pacemaker

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underlying rhythms (4), and testing the effects of social cues at different times of day (20,22,23). However, they neglected to test the relevance of such cues for entraining rhythms in the natural environment. To evaluate the potential usefulness of social cues as a zeitgeber, one must demonstrate that these cues can exert independent effects on biological rhythms in the presence of a light-dark (LD) cycle.

To date, animal models of social entrainment have been developed in either nocturnal, asocial species or birds that do not live in groups during much of the year (5,6,11,19,22,23). The experiments presented here investigate the effects of social cues on the synchronization of a communal-living, diurnal species, *Octodon degus*, in which social cues likely have ecological relevance.

*Octodon degus* is a South American hystricomorph rodent, active throughout the year and diurnal in both the natural environment and the laboratory (17,28), with peaks of general activity occurring in the morning and/or late afternoon and temperature minimum occurring about 2.5 h prior to activity onset. Degus also possess a complex social organization consisting of small colonies of extended family groups (13), including both males and females, in which females rear young in a communal fashion in the field (9,28) and in the laboratory (Goel, unpublished).

Social interaction studies with degus have yielded differences in behavior between the sexes. Females are reported to be non-aggressive. They facilitate social contact via olfactory communication (8) and scent-marking behavior (14), and can discriminate both male and female urine from other stimuli (7). In contrast, males have been reported to be aggressive and avoid social contact (8). They scent-mark less frequently than females (14), and are unable to discriminate male urine from other stimuli (7). These data suggest that female degus may be more responsive than males to olfactory cues.

The following two experiments test whether social interaction can accelerate the rate of resynchronization of the circadian activity and core body temperature rhythms following a phase advance for degus housed in a light-dark (LD) cycle. In addition to photic cues, social cues may be a powerful synchronizing agent for an animal housed with a conspecific; light is the primary entraining agent when an animal is housed alone. Since urine and scent marking are used by degus to mark the environment around their burrows and to mark conspecifics, sex differences in discriminatory ability (7,14) could lead to sex differences in sensitivity and response to conspecific social cues. Based on sex differences in social communication, we predicted female degus housed with female conspecifics would resynchronize faster than all other groups, and males housed with male conspecifics would resynchronize slower than all other groups.

#### METHOD

##### General Methods

**Subjects.** Twenty-six sexually mature male and female *Octodon degus* were chosen for these studies. The experimental subjects were born in a laboratory colony at the University of Michigan and were chosen based on age and sex. The age of subjects ranged from 6 mo to 3 yr (average lifespan is 5–7 yr). Prior to this experiment, all animals were housed in LD 12:12, lights on at 0600 h.

All animals were maintained on a diet of Purina Rodent Chow and Guinea Pig Chow supplemented weekly with apples and peanuts. Both food and water were available ad lib. Initially, the animals were individually housed in 42.5 × 22 × 19 cm cages either in an open room or in ventilated, light-tight boxes. Following initial phase-shifting and entrainment, the animals were

housed in large cages (42.5 × 46 × 19.5 cm) with a wire mesh divider placed in the middle. The divider prevented physical contact between animals on opposite sides of the divider (e.g., aggression or mating), but still allowed visual, olfactory and auditory communication.

**Data collection.** Mini-mitter transmitters were used to monitor core body temperature and general activity (Mini-mitter, Inc., SunRiver, OR). General activity recorded any movement an animal made in the cage. Temperature and general activity were recorded and stored in 10 min bins by Dataquest III (Mini-mitter, Inc., SunRiver, OR).

**Procedure.** Transmitters were surgically implanted in the peritoneal cavity of each animal. Degus were anesthetized with an intraperitoneal injection of Xylazine (.01 ml of Xylazine/100 g body weight) and Ketamine HCL (.12 ml of Ketamine/100 g body weight). Yohimbine (.01 ml of Yohimbine/100 g body weight) and 5 ml lactate ringers were administered subcutaneously immediately after surgery to facilitate recovery.

##### Experiment 1

This experiment was designed to test the effects of social cues on the rate of resynchronization in a general population of male and female degus. Table 1 indicates the experimental groups and number of animals used for each condition.

All animals were housed in LD 12:12, lights on at 0600 h during the postoperative recovery stage. One week following surgery, the animals were randomly selected to become either phase-shifters (animals to be given an initial 6-h phase delay followed by a 6-h phase advance) or phase-donors (animals to remain on the original LD cycle). Phase-shifters were moved into light-tight boxes and maintained on LD 12:12, lights on at 1200 h. Thus, these animals were exposed to a 6-h delay. Phase donors remained in the open room in LD 12:12, lights on at 0600 h. Three weeks following the 6-h delay, the phase-shifters were moved from their light-tight boxes into the testing room with the phase-donors, thus being exposed to a 6-h phase advance. At this time, animals were moved from their individual cages into the large cages with mesh dividers in the testing room and were housed in one of three ways (see Table 1). Phase-shifters were placed on one side of a large cage divided by hardware mesh with (i) a donor animal on the other side; (ii) another phase-shifter on the other side; or (iii) housed alone on one side of the divided cage.

Throughout the experiments, female estrous periods were monitored. In the degu, the estrous cycle is 18–21 days in length (17). Estrus was identified behaviorally as an increase in activity and body temperature sustained for a 24–36 h period (17).

##### Experiment 2

This experiment was designed to assess the effects of social cues on the rate of resynchronization in a random subset of the population used in Experiment 1. Unlike Experiment 1, Experiment 2 eliminated between subjects variation by examining the effects of social cues on individuals tested in both the control group and one of the four donor-phase-shifter groups. Thus, an individual's rate of resynchronization with and without social cues could be assessed. Table 1 describes the experimental groups and number of animals used in each group.

##### Data Analysis

Data were collected for 3 wk following the initial 6-h delay. Temperature and general activity actograms were analyzed to determine that phase-shifters had resynchronized to the initial

TABLE 1  
THE EXPERIMENTAL DESIGNS FOR EXPERIMENTS 1 AND 2

Group	Pair	N
Experiment 1		
Donor: Phase-shifter	Female:Female (FF)	(5)
	Female:Male (FM)	(7)
	Male:Male (MM)	(6)
	Male:Female (MF)	(5)
	Phase-shifter: Phase-shifter	(4)
Phase-shifter: Phase-shifter	Male:Male (MM)	(4)
	Female:Female (FF)	(3)
Phase-shifter Alone	Male (M)	(3)
	Female (F)	(3)
Experiment 2*		
Donor: Phase-shifter; Control	Female:Female (FF); Female Control (FC)	(4)
	Female:Male (FM); Male Control (MC)	(4)
	Male:Male (MM); Male Control (MC)	(3)
	Male:Female (MF); Female Control (FC)	(4)

\* Note: The same animal was a phase-shifter in both the control and donor: phase-shifter conditions.

phase delay in preparation for the experimental manipulations. Activity and temperature typically reentrain within 14-18 days (17). Therefore, the phase-shifters remained in LD 12:12, lights on at 1200 h, for a total of 3 wk to allow sufficient time for complete resynchronization of all circadian rhythms. Following the 6-h advance in the presence or absence of social cues, both donor and phase-shifter activity and temperature rhythms were monitored for 3 wk.

Actograms were used to determine the rate of resynchronization, defined as the length of time (number of days) it took for the activity and temperature rhythms of each phase-shifter to reestablish its previous phase relationship (i.e. the coordination of specific times between a biological rhythm and a zeitgeber) to the new lighting schedule. For these experiments, resynchronization for animals housed with conspecifics could occur either through entrainment of the pacemaker or via a masking effect of the circadian rhythms. However, for animals housed alone, the rate of resynchronization of rhythms by the light-dark cycle is assumed to be via entrainment of the pacemaker.

Resynchronization was assessed for the temperature rhythm by monitoring the daily temperature increase following the daily temperature minimum (see Fig. 1). Temperature minimum is defined as the time of the lowest temperature of the day and occurs during the temperature trough approximately 3 h prior to lights on in entrained animals. Resynchronization of the activity rhythm was evaluated by monitoring activity onset (see Fig. 1), defined as the time when the majority of activity for the day began (activity onset is 20 min of activity after a minimum 4 h hiatus of activity in entrained animals). Therefore, for these experiments, an animal was considered resynchronized when its temperature minimum and activity onset components had advanced and reached their previous phase angle relationship to the new light-dark cycle. The resynchronization rate of each rhythm was considered separately; thus it was possible for the rhythms to complete resynchronization on different days (and therefore, at slightly different rates).

To increase reliability, two people, blind to the treatment groups, independently analyzed the data to determine the rate of resynchronization. The concordance rate was 84% for both the temperature and activity rhythms. For the 16% of temperature or activity cases for which concordance did not occur, the two raters

discussed each individual case, blind to its treatment group, and arrived at a consensus as to the day resynchronization occurred for that particular rhythm. Data are presented as mean  $\pm$  SEM.

In Experiment 1, one way analysis of variance (ANOVA) and post-hoc *t*-tests were used for statistical analysis. In Experiment 2, paired *t*-tests were used to assess changes in individual rates of resynchronization in control or social conditions. For both experiments, changes in mean activity levels as well as temperature and activity amplitude (the difference between the mean and maximum values) for the first five days following the phase shift were assessed using multivariate repeated measures analysis. The two-day preshift baseline values for all groups were compared using one way analysis of variance. *P* values less than 0.05 were considered significant.

## RESULTS

### Experiment 1

There were no significant differences for either females or males in the rates of resynchronization of the temperature or activity rhythms between phase-shifters housed with other same sex phase-shifters and phase-shifters housed alone. Thus, the presence of another phase-shifting animal did not affect the rate of resynchronization of its partner. The data of phase-shifters from the two control groups were combined to form one male and one female control group for further statistical analyses ( $N = 7$  males, 6 females).

Temperature resynchronized 36.8% faster (Fig. 2A;  $p < 0.05$ ) and activity resynchronized 31.0% faster (Fig. 2B;  $p < 0.05$ ) for female phase-shifters paired with female donors (FF group) than for females housed in the control condition. Females also resynchronized the temperature rhythm 41.8% faster when placed with female (FF) rather than male donors (MF;  $p < 0.02$ ).

There were no differences in the rate of resynchronization between the three male phase-shifter groups for the temperature (Fig. 3A) or activity rhythms (Fig. 3B). Males did not respond differentially to the presence of either male or female donors.

The activity rhythm of male controls reentrained 16.6% faster ( $10.1 \pm 2.7$  days vs.  $13.3 \pm 1.2$  days) than that of female controls ( $p < 0.03$ ). The temperature rhythm also tended to reentrain

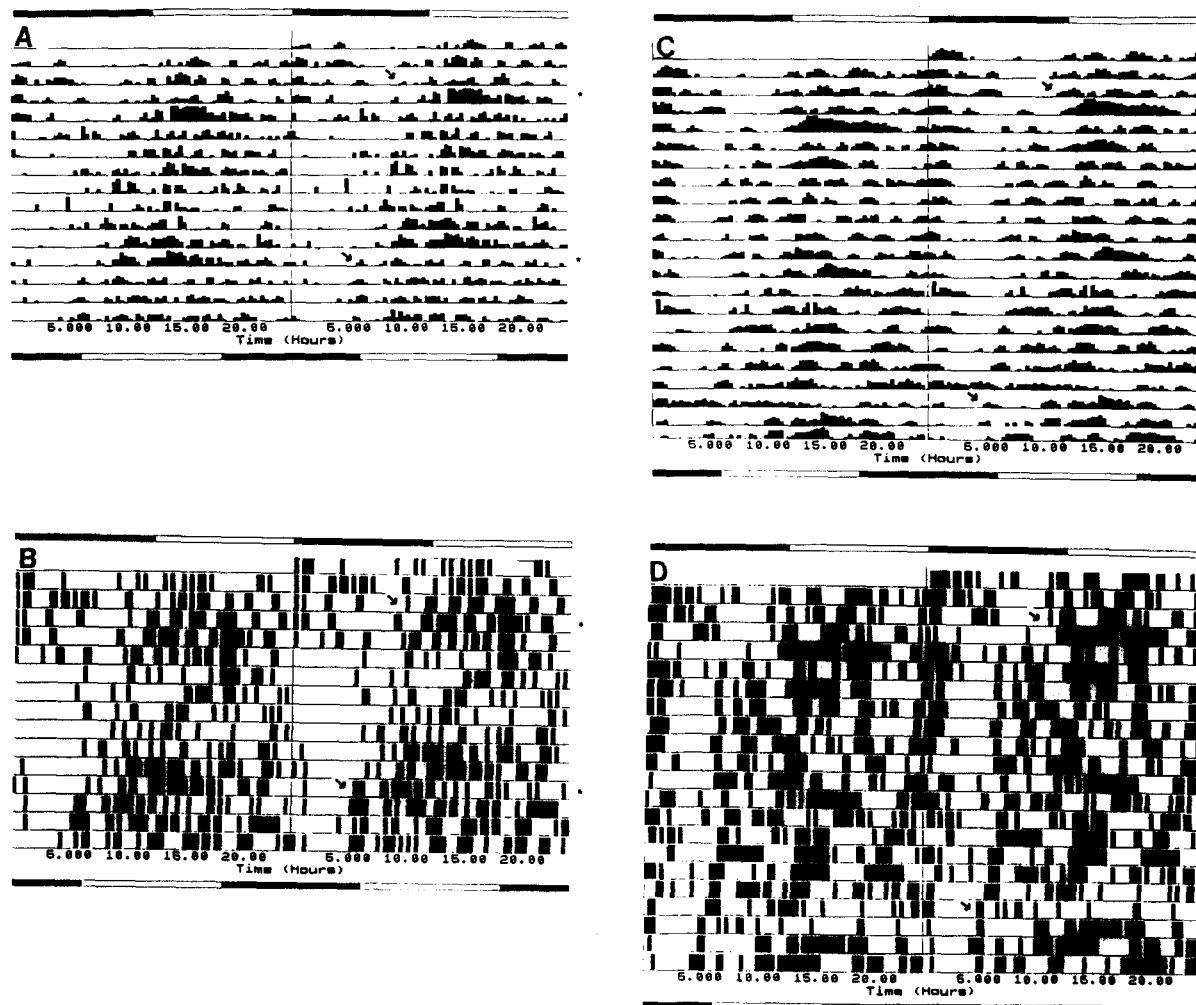


FIG. 1. Double-plotted temperature and general activity actograms for a female phase-shifter housed with a female donor (A and B, respectively) and for a female phase-shifter housed alone (C and D, respectively). The top light-dark bar indicates LD 12:12, lights on at 1200 h. The lowest 30% of temperature and activity values are cut from the figure for ease in viewing the daily temperature rise and activity onset. The first asterisk in the right margin indicates the day of the phase shift (6 h advance) and the first arrow indicates the phase angle prior to the shift. The bottom light-dark bar indicates the new lighting schedule. The second asterisk in the right margin denotes the day of resynchronization as marked by the reestablished phase angle (second arrow).

faster for males, but was not significantly different from the female mean ( $10.3 \pm 2.6$  days vs.  $12.3 \pm 1.8$  days;  $p = 0.12$ ).

There were no differences in the two-day preshift baseline levels for mean activity, temperature or activity amplitude between groups. There were also no significant differences between or within the four donor groups or four phase-shifter groups for changes in activity or temperature amplitude for the five days following the 6-h phase advance.

Following phase shifts, the phase-shifter groups displayed increases in mean activity from preshift baseline values. Multivariate repeated measures analysis for the five days following the shift revealed no significant differences in mean daily activity between the four phase-shifting groups paired with donors.

The donor groups also displayed increases in mean activity from preshift baseline values following pairing with phase-shifting animals. Multivariate repeated measures analysis indicated a significant interaction across days and between the donor groups. Between the four donor groups, mean activity levels for female donors housed with female phase-shifters (FF) were significantly

higher on day two following the shift (see Fig. 4B;  $p < 0.03$ ) and approached significance for the day of the shift ( $p = 0.10$ ) compared with the other three donor groups. In addition, female donors housed with female phase-shifters (FF) had higher levels of activity than male donors housed with female phase-shifters (MF) across all days (see Fig. 4B;  $p < 0.001$ ). The FF donors also displayed higher levels of activity across all days, which approached significance, compared with male donors housed with female phase-shifters (FM) (see Fig. 4B;  $p < 0.06$ ).

There was no effect of estrus on the rate of resynchronization of activity or temperature for animals in any group. None of the phase-shifting females underwent estrus during their phase-shifts; estrus occurred prior to or following resynchronization.

#### Experiment 2

As in Experiment 1, no differences in the rates of resynchronization of the temperature or activity rhythms emerged for males or females phase-shifting with another same sex phase-shifter

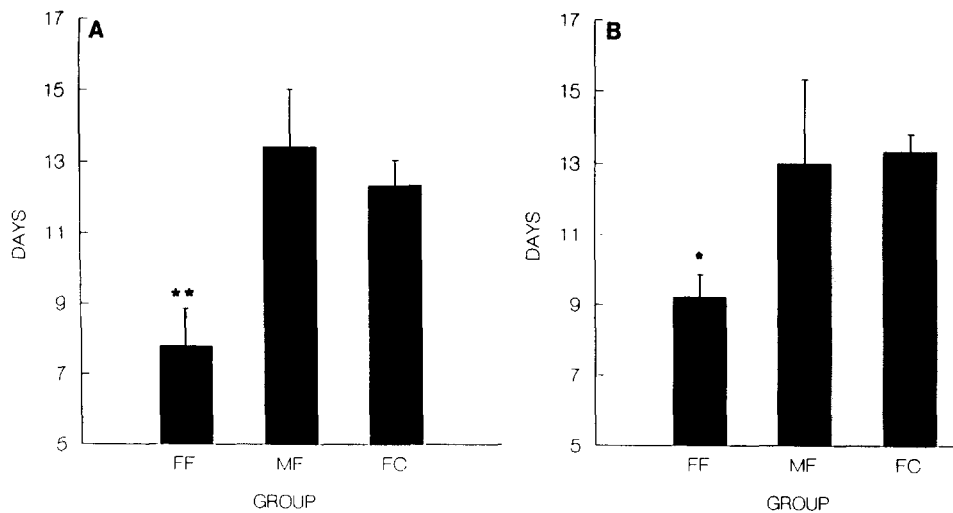


FIG. 2. The mean ( $\pm$ SEM) number of days required for resynchronization of the temperature rhythm (A) and activity rhythm (B) for female phase-shifters. FF = female donor, female phase-shifter; MF = male donor, female phase-shifter; FC = combined control group of females phase-shifting with another female and females phase-shifting alone. \* significantly less than control group; \*\* significantly less than all other groups,  $p < 0.05$ .

and for those shifting alone. The presence of another phase-shifter did not enhance the rate of resynchronization. For further statistical analyses, males and females housed in either of the above conditions were treated as controls to conduct paired comparisons with these same animals when they were housed with a donor.

When an individual female's rate of resynchronization was compared after being housed in control conditions and after being placed with another female, the results from Experiment 1 were repeated. Temperature resynchronized 39.4% faster (Fig. 5A;  $p < 0.03$ ) and activity resynchronized 30.2% faster (Fig. 5B;  $p < 0.02$ ) when female phase-shifters were paired with female donors than when phase-shifters were housed alone.

In contrast, both the temperature and activity rhythms in females tended to resynchronize more slowly when placed with male donors (MF) than when housed in control conditions. However, only the temperature rhythm (Fig. 6A; temperature:  $p < 0.02$ ; activity:  $p = 0.28$ ) differed significantly between the MF and FC conditions.

As in Experiment 1, there were no differences for the rate of resynchronization of the temperature or activity rhythms between the males phase-shifting in the control condition and those paired with either male or female donors. Thus, male resynchronization is unaffected by this particular presentation of social interaction.

As in Experiment 1, there were no significant differences in activity or temperature amplitude between or within the four

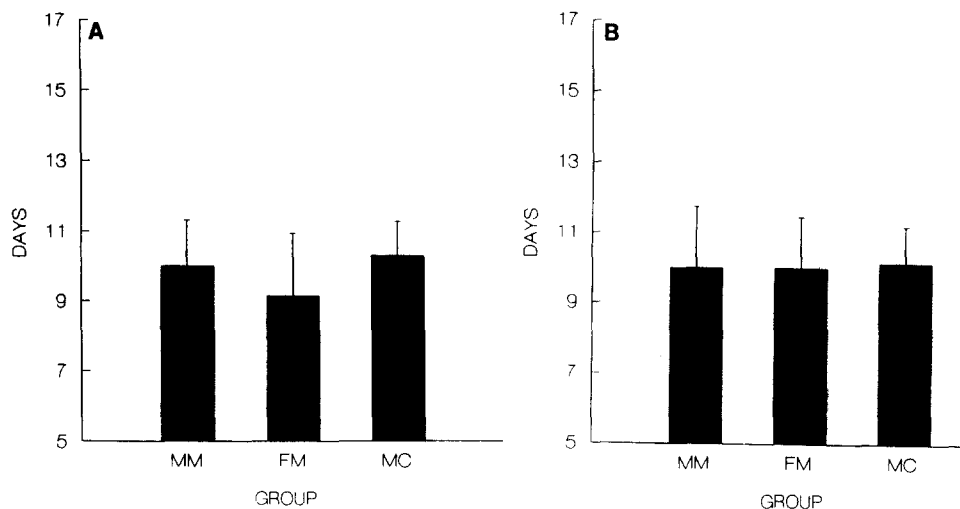


FIG. 3. The mean ( $\pm$ SEM) number of days required for resynchronization of the temperature rhythm (A) and activity rhythm (B) for male phase-shifters. MM = male donor, male phase-shifter; FM = female donor, male phase-shifter; MC = combined control group of males phase-shifting with another male and males phase-shifting alone.

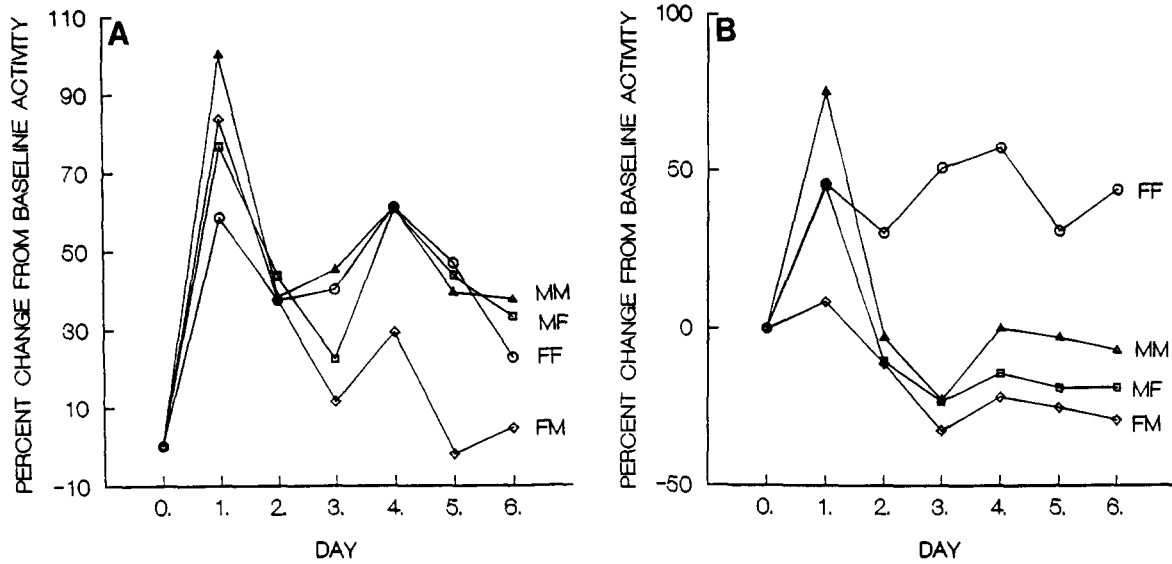


FIG. 4. Percent change from baseline activity for phase-shifters (A) and donors (B). Day 0 represents two days of preshift, baseline activity; Day 1 is the day of the shift; Days 2–6 are postshift days. See Figs. 2 and 3 for group designations. Donor FF animals have significantly elevated activity levels compared to all other donor groups. Phase-shifter FM animals have significantly lower activity levels than phase-shifters in the MF group. Other donor or phase-shifter groups did not differ significantly.

phase-shifter groups (housed with donors) for the five days following the 6-h phase advance. There were also no differences in the preshift baseline levels for mean activity and temperature or activity amplitude among the groups. While there were no significant differences in mean activity between phase-shifters over the five postshift days, mean activity levels did decrease over the five days.

Similar to the results of Experiment 1, there was no effect of estrus on the rate of resynchronization of the phase-shifting females. Once again, estrus occurred prior to or following resynchronization.

DISCUSSION

The results from these two experiments indicate that the presence of entrained conspecifics can alter the rate of resynchronization to a large phase shift in the social, diurnal *Octodon degus*. Moreover, there appears to be a sex difference in response: the rate of resynchronization of females was enhanced by female donors and delayed by male donors, whereas males were not affected by either sex donor. This was true of the population at large as well as for individual animals who were tested in both the control and experimental conditions. In addition, males housed alone or with other phase-shifting males displayed an

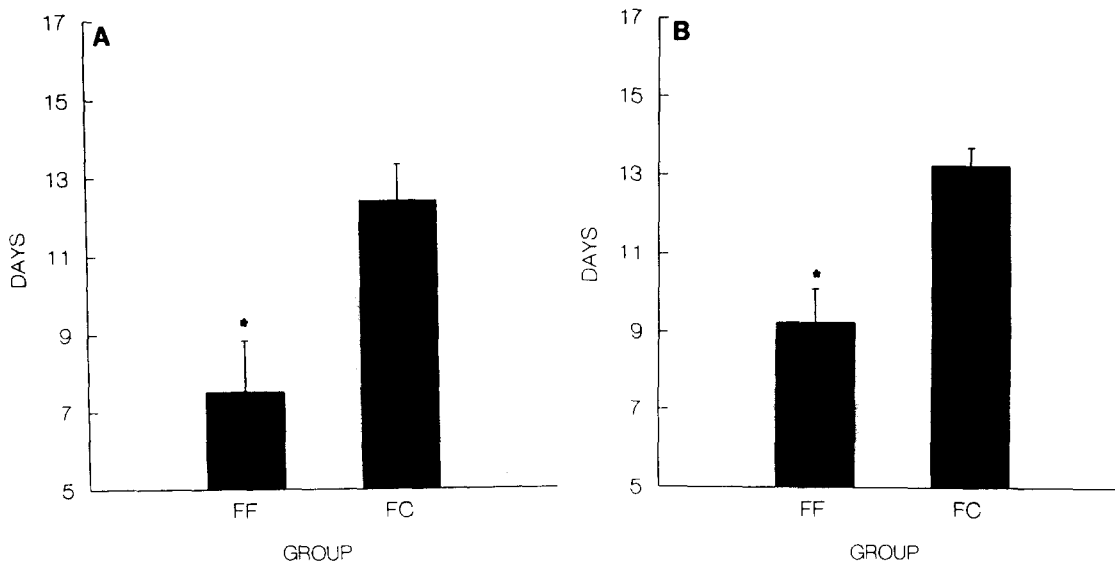


FIG. 5. The mean ( $\pm$ SEM) number of days required for resynchronization of the temperature rhythm (A) and activity rhythm (B) for the same females when housed with another female (FF) or when housed alone (FC). Symbols as in Fig. 2.

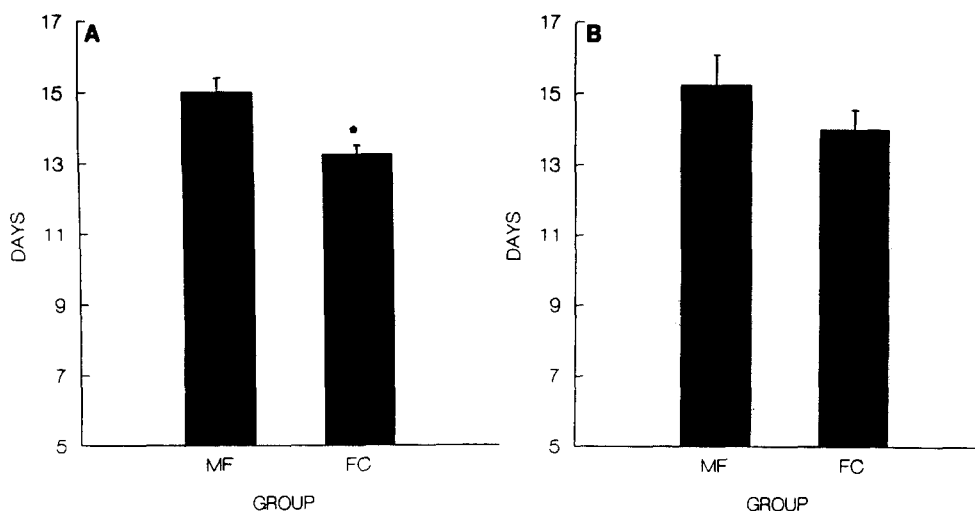


FIG. 6. The mean ( $\pm$ SEM) number of days required for resynchronization of the temperature rhythm (A) and activity rhythm (B) for the same females when housed with a male (MF) or when housed alone (FC). \* significantly less than experimental group,  $p < 0.05$ .

accelerated rate of reentrainment following 6-h advances of the light-dark cycle compared to females in the same conditions.

In these studies, female phase-shifters housed with female donors resynchronized 30–40% faster than females in the control conditions. Male phase-shifters did not increase their rates of resynchronization when housed with either male or female donors. The observed sex difference in response to being housed in close proximity to an entrained animal during a phase advance could be attributed to an increased sensitivity to social cues in females. Urine and scent marking are used by females to mark the environment around burrows as well as to mark conspecifics (7,14), and females attend to these cues more than males (7). It seems plausible that differences in discriminatory ability between males and females could lead to differences in sensitivity and response to conspecific social cues during the resynchronization period.

It is important to consider the possibility that social cues may be masking the phase of the activity and temperature rhythms rather than directly affecting the pacemaker. We believe that social cues indeed are resetting the pacemaker, as most animals displayed no obvious masking of their temperature or activity rhythms, and the rhythms resynchronized at nearly the same rate. Furthermore, our definition of resynchronization includes a reestablishment of the original phase angle between the light-dark cycle and each circadian measure, thus eliminating the possible effects of masking on our resynchronization data. However, to truly test pacemaker phase, animals must be placed in constant conditions and free-running rhythms monitored at the point at which entrainment by social cues is postulated to occur. This experiment is currently being conducted by the investigators.

The sustained increase in the degus' mean activity following phase shifts is consistent with an increase in wheel-running activity after phase shifts reported for the golden hamster (22). However, it appears that increases in overall mean activity are not directly responsible for increases in the rate of resynchronization, because no differences exist between any of the four donor-phase-shifter groups. Thus, changes in the rate of resynchronization are likely being expressed as behaviors not detected by this particular measure of increased activity. It is possible that increases in a particular activity at certain times of the circadian

day, rather than an overall increase in activity, are important for affecting the resynchronization rate of phase-shifters.

Interestingly, donor levels of mean activity did differ between groups. Donors from the female donor-female phase-shifter (FF) group displayed sustained increases in activity level as compared with the three other donor groups. The phase-shifting females from the FF group had accelerated rates of resynchronization. Thus, it seems plausible that female donors are engaging in a behavior or repertoire of behaviors which influence their partner's rate of resynchronization in unknown ways.

Differing rates of resynchronization were not correlated with changes in temperature or activity amplitudes. These results are similar to previous findings in the degu following phase shifts. However, unlike Labyak (17), who reported increases in temperature amplitude following 6-h advances, in these experiments there were no significant changes in body temperature amplitude after 6-h phase advances. Differences between the studies could be due to differences in experimental design: in the experiments reported here, animals were housed without running wheels, with a conspecific, and engaged in social interaction, whereas Labyak's animals (17) were housed individually with running wheels.

The fact that degus' temperature and activity rhythms following phase shifts did not undergo changes in amplitude was unexpected. Aschoff (2) suggests that phase shifts of the light-dark cycle lead to decreases in activity and temperature amplitudes. Decreases in amplitude have been reported for temperature (10) as well as various performance tasks (10,15) in humans following phase shifts. Smaller amplitudes suggest a weakening of the association or coupling between an entrainer and a particular circadian rhythm. This weakening has been postulated to expedite the shifting of the clock because rhythms are less stable following phase shifts (32). Our data suggest that decreases in amplitude are not necessary for acceleration in the rate of resynchronization to occur.

Estrus did not influence the rate of resynchronization. Among donor females, there were only two cases in which estrus occurred during the partner's phase shift. In both cases, the phase-shifters resynchronization was equivalent to the group average. Throughout the experiments and across different groups, female

phase-shifters and donors were in different phases of their estrous cycles, thus limiting the effects of hormones and related factors on their rates of resynchronization. Davis et al. (4) also reported that estrus did not influence rates of resynchronization in golden hamsters.

Control males reentrained significantly faster than control females for the activity rhythm and approached significance for the temperature rhythm. This finding was unexpected, but similar data have been reported previously in other species. Davis et al. (4) reported that golden hamsters displayed sex differences in several aspects of the circadian control of wheel-running activity. Males entrained better at the upper limit of their range of entrainment, had a longer free-running period, had a different phase response curve to light and had a later phase angle of entrainment. Wever (30,31) reported a circadian sex difference in humans. Females had a shorter free-running period for the sleep/wake rhythm compared to males, but had equivalent free-running periods for the temperature rhythm. Finally, Schull et al. (25) found a similar sex difference in Sprague-Dawley rats: females had shorter free-running circadian periods than males for wheel-running activity.

Unlike Davis et al. (4), we did not find a significant difference between males and females in the phase angle of entrainment for either activity onset or temperature rise. However, Labyak and Lee (unpublished) have found that male degus have a shorter free-running activity period than females (males =  $23.2 \pm .1$  h, females =  $23.7 \pm .1$  h;  $p < 0.001$ ) in constant darkness (DD), possibly making it easier for males to phase advance. Since females have longer free-running periods than males, we may find that they will reentrain faster to delays than males. Besides differences in period length, it is also possible that males and females have different phase response curves for light, with males perhaps generating larger phase advances than do females.

Although the results from the reported two experiments indicate that female degus are responsive to social cues following large phase advances, these shifts do not occur naturally in the life of a degu. The shifts were used in these experiments as tools to investigate responses to a significant light change in a social

species. The degu, unlike many other existing animal models, shares many characteristics in common with humans, including its diurnality, its highly social nature, and its similar activity and temperature patterns (17). Because of these commonalities, the degu serves as a valuable model for (i) understanding how non-photic and photic entrainers may interact to entrain or synchronize circadian rhythms, and (ii) addressing circadian questions that relate to humans (20), including jetlag and shiftwork.

In a species which is territorial and highly social, one might expect that social cues would prove beneficial and perhaps necessary for communication among conspecifics. For example, females who originally used social cues as a means of communication, probably show increased sensitivity to these cues and may be able to co-opt these cues for other purposes, such as entraining agents. On the other hand, a similar mechanism would not be expected to exist for a virtually asocial species, in which social interaction between conspecifics is very limited. In asocial species, the ability to respond to naturally occurring, nonaggressive social stimuli may not be necessarily advantageous, and the influence of social cues as entrainers may be negligible.

These studies tested whether social cues influence the synchronization of circadian rhythms; they did not address the mechanism(s) by which these cues operate. Future experiments must be done to determine whether olfactory, visual, or auditory cues are important for the degu and for the observed sex differences in response to these cues. In addition, these studies only tested the effects of social cues following phase advances. Social cues may have entirely different effects on resynchronization following phase delays or with smaller or larger phase advances. Males may be unresponsive only in the limited conditions we presented and may prove to be quite responsive when tested in other conditions.

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