

# Ovarian hormones influence olfactory cue effects on reentrainment in the diurnal rodent, *Octodon degus*

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## Abstract

*Octodon degus*, a social hystricomorph rodent, responds to olfactory cues from a gonadally intact female entrained to a light–dark cycle (LD) by accelerating reentrainment of running wheel activity following a 6-h phase advance of the LD cycle. In this study, we examined the role of ovarian hormones in the production of and responsiveness to olfactory social cues in females. Experiment 1: intact females were sequentially phase-advanced 6 h with photic cues alone, or in the presence of an intact female donor, ovariectomized (OVX) donor, a castrated male, or a castrated male with testosterone replacement. Acceleration of reentrainment occurred only in the presence of the intact female donor while reentrainment was delayed by OVX donors. Experiment 2: OVX females undergoing a 6-h phase advance did not accelerate reentrainment in the presence of an intact female donor compared to reentrainment with photic cues alone. Thus, ovarian hormones are necessary for both the production of and responsiveness to olfactory cues. Experiment 3: OVX females implanted with estrogen-filled Silastic capsules did not accelerate reentrainment following the 6-h phase advance in the presence of an intact donor, whereas animals implanted with a combination of estrogen- and progesterone-filled capsules (Experiment 4) reduced the length of time needed to reentrain in the presence of an intact donor. Therefore, combined progesterone and estrogen are sufficient for responsiveness to the effective olfactory cue in intact donor females. These data clarify that the sex difference in sensitivity to non-photoc odor effects on circadian reentrainment is caused by both the testosterone's inhibitory effects (*Octodon degus*. J. Biol. Rhythms 18 (2003) 43–50) and the enhancing effects of progesterone and estrogen.

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## Introduction

Circadian rhythms are the manifestations of important biological timing mechanisms for multicellular organisms. They allow an organism to occupy a specific niche in the environment and to prepare for various daily activities at optimal times for the organism's success. Circadian rhythms are synchronized or entrained to an approximately 24-h period by environmental stimuli that occur on a daily cycle. The light–dark (LD) cycle is the most commonly used zeitgeber (“time giver”), although many non-photoc stimuli can be used as zeitgebers either alone or in conjunction with a LD cycle.

Olfactory social cues from conspecifics can act as non-photoc zeitgebers that aid entrainment or reentrainment after a phase shift. Reentrainment is the reinstatement of entrained rhythms typical for an individual after a change in the zeitgeber (e.g., transmeridian jet travel that can result in jet lag). In this study, we examine the role of ovarian hormones on the ability of female *Octodon degus* to produce and respond to olfactory cues that accelerate reentrainment following a 6-h phase advance of the LD cycle.

Degus are social and diurnal hystricomorph rodents native to South America. They lend themselves well to studies of circadian rhythms and olfactory social cues because they produce olfactory cues and rely on olfaction to communicate in their natural environment (Davis, 1975; Fischer and Meunier, 1985; Fischer et al., 1986) and in the laboratory (Goel and Lee, 1996; Kleiman, 1975).

The ability of the degus to use social cues to accelerate the rate of reentrainment following a 6-h phase advance of the light cycle was first reported by Goel and Lee (1995a).

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Although male degus reentrain significantly faster than females following a phase advance of the light cycle when using only photic cues, they found that female degus, but not males, were able to reentrain 30–40% faster after a 6-h phase advance when in the presence of a previously entrained female social cue donor (henceforth called “donor”). Furthermore, a female that was also undergoing a phase shift with the experimental animal (“shifter”) did not provide the necessary stimulus for acceleration of the reentrainment rate. Thus, only an entrained female donor produced the effective odor and the phase of the estrous cycle did not correlate with the effect (Goel and Lee, 1995a,b). To confirm that the stimulus was olfactory, females were bulbectomized and then phase-advanced 6 h with a female donor. Bulbectomized animals did not shorten their time to reentrain when exposed to odors compared to when they were housed alone with only photic cues present (Goel et al., 1998). Governale and Lee (2001) further refined the nature of the stimulus by passing odors from a closed unit housing female donors to units containing animals undergoing a phase shift. The routed odors were sufficient to shift and entrain females in the experimental group.

Male degus did not enhance their reentrainment rate in the presence of a female donor in the original study of social cues and 6-h phase advances of the light–dark cycle. To determine whether males had the capability to respond to the olfactory stimulus, the strength of the cues was increased by using two females instead of one (Jechura et al., 2003). The males responded to the presence of multiple entrained females with shorter reentrainment rates compared to shifting alone. Thus, males could respond to the olfactory cues, but they had a higher threshold for the stimuli. The study was refined further to examine possible proximate reasons for the males’ need for multiple donors. We found that testosterone suppressed the males’ responsiveness to olfactory cues. Castrated animals accelerated their rate of reentrainment when shifted with odors from a single intact female and were once again unresponsive when implanted with testosterone capsules and phase-advanced in the presence of a single donor. Thus, testosterone was found to be an important factor for males in the use of olfactory cues to speed reentrainment.

The effect of testosterone on the ability to reentrain faster in the presence of olfactory social cues was also tested in females. Testosterone implants in females resulted in a loss of responsiveness to the reentrainment-accelerating effects of previously effective olfactory cues (Jechura et al., 2003). This indicated that the brains of males and females are not different in their responsiveness to testosterone’s inhibitory effects on odor-induced accelerated reentrainment.

Little is known about the role of ovarian hormones in the process of hastened reentrainment with olfactory cues except that the female donor must be entrained to provide the appropriate stimuli (Goel and Lee, 1995a). In this study, we tested the hypothesis that ovarian hormones are necessary for the production of and response to reentrainment-accelerating

olfactory cues by testing the donor animals’ effectiveness and shifting animals’ responses before and after ovariectomy.

Alternatively, ovarian hormones may not be necessary in the production of donor cues, and males might also be able to produce the cue if their testosterone is removed. To determine whether a castrated male can be an effective donor, we tested phase-advancing intact females in the presence of castrated male donors and testosterone-replaced castrated male donors. We hypothesized that the phase-advancing females would not accelerate their rate of reentrainment in the presence of a castrated male based on our first hypothesis that ovarian hormones are necessary for the production of effective olfactory cues.

In the third and fourth experiments, we examine the nature of the ovarian hormonal cue that is being used by shifting females to increase their rate of reentrainment. If ovariectomized (OVX) females are unresponsive to the accelerating effects of a donor, then replacing the ovarian hormones might reinstate responsiveness. We implanted estrogen or a combination of estrogen and progesterone capsules into OVX females and tested their responsiveness to an intact female donor. We hypothesized that exposure to a donor implanted with estrogen alone would not be sufficient to reduce the length of time to reentrain after a 6-h phase advance because previous data have shown that the olfactory cue donors are unlikely to be in estrus more than once, if at all, during a reentrainment period (Goel and Lee, 1995a; Jechura and Lee, unpublished data). Degus have a relatively long estrous cycle of approximately 21 days (Labyak and Lee, 1995) with only 4–7 days of elevated estradiol, thus providing a relatively short exposure to high estrogen levels during an entrainment period. We predicted that the combination of estrogen and progesterone would reinstate the OVX females’ responsiveness to the accelerating effects of olfactory cue donors. Donor females provide more days with higher progesterone levels than estrogen (14 days per cycle; Labyak and Lee, 1995). We chose to use a combination of estrogen and progesterone and not progesterone alone because progesterone has little effect unless the receptors for it are first increased by prior exposure to estrogen. Estrogen capsules provided constant estrogen levels sufficient to maintain progesterone sensitivity. Injection of estrogen before implanting progesterone capsules rather than use of continuous estrogen implants was not feasible because of the stress and disruption to the circadian rhythms that occur in degus with repeated handling and injections (Governale and Lee, unpublished data).

## Methods

All methods were consistent with previous experiments examining the effects of olfactory social cues and reentrainment after a 6-h phase advance of the LD cycle (Jechura et al., 2000, 2003). In brief, animals were obtained from an outbred colony maintained at the University of Michigan.

Before use in the experiments, all animals were maintained at  $18 \pm 1^\circ\text{C}$  on a LD 12–12 light schedule, with lights on at 0600 h and off at 1800 h. All experiments used adult animals, 2–4 years old, with an average life expectancy of 6–8 years. The animals were housed individually in  $48 \times 26.7 \times 20.3$  cm Nalgene cages with running wheels (9-cm wide, 34.5-cm diameter). Cages were cleaned weekly at varying times during the light phase of the LD cycle. Rodent chow (Purina 5001) and water were available ad libitum. All procedures involving animals were approved by the Animal Care and Use Committee (IACUC) at the University of Michigan.

Surgical procedures for ovariectomy (OVX) and castration (CAST) were carried out with Ketamine HCl (30 mg/kg of body weight) and Xylazine (2.5 mg/kg of body weight) anesthesia. Yohimbine (2.5 mg/kg of body weight) and lactated ringers (3 ml, ip) were used to aid recovery. All degus were allowed 1 week for recovery before entering the experiment.

During reentrainment, animals were housed in pairs, with the phase-shifting animal and the social cue donor separated by a wire mesh divider in a Nalgene cage with dimensions of  $48 \times 38 \times 19.5$  cm (Goel and Lee, 1995a,b). Data were collected as running wheel rotations per 10-min blocks using Minimitter equipment and Vitalview software (Minimitter, Inc., Sun River, OR). Data collection began 3 days after introduction of the wheels, allowing the animals to become familiar with the apparatus.

Social cue donors in Experiments II–IV were intact while the hormonal state of the shifters was manipulated. In Experiment I, the donor cues were manipulated and the shifting animals were intact. In all cases, donors were randomly paired with an unrelated and unfamiliar shifting animal at the time the phase shift occurred. Phase advances were always achieved by having the new “lights on” occur 6 h early on the first day of the shift. Thus, the last night on the old LD cycle was shortened by 6 h.

## Procedures

### Experiment I

Eight intact adult female degus were subjected to five 6-h phase advances in the LD cycle and allowed to fully reentrain between shifts. First, they shifted with only photic cues (control), then in the presence of an intact female (positive control), an OVX female, a castrated male, and lastly with a castrated male with a testosterone implant (negative control). Previous counter-balanced designs and analyses have demonstrated that there are no order effects on rates of reentrainment as long as complete recovery is achieved between shifts (Governale and Lee, 2001; Jechura et al., 2003).

### Experiment II

Eight intact adult females, different from those in Experiment I, were allowed to reentrain alone and again in the

presence of a female social cue donor following a 6-h phase advance of the LD cycle. The shifting females were then OVX and given 1 month for the effects of ovarian hormones to be eliminated, as determined by a lack of estrous cycles. They were then phase-advanced 6 h and allowed to reentrain with and without an intact female social cue donor to compare responsiveness to olfactory cues before and after OVX.

### Experiment III

Eight adult OVX females (different from those in the first two experiments) were phase-advanced 6 h with and without olfactory cue donors to obtain baseline data. They were then implanted with Silastic capsules containing crystalline estradiol benzoate (EB; Sigma) 48 h before the next phase shift. Capsules were prepared as described in Labyak and Lee (1995) with an effective length of 15 mm (Dow-Corning; 1.98 mm ID, 3.15 mm OD). Vaginal opening consistent with estrus was induced. Phase advances with and without the presence of intact female donors were repeated. The length of time to reentrainment was compared before and after EB replacement.

### Experiment IV

Eight OVX females from Experiment II were implanted with two Silastic capsules, EB and progesterone (P; Sigma), 48 h before the shift. The P capsules were equivalent to those used by Labyak and Lee (1995) and prepared as described above for EB. The progesterone was sufficient to prevent vaginal opening despite the presence of EB. The 6-h phase advances with and without intact donors present were repeated. The number of days to reentrain was compared between treatments. Two animals were eliminated from the experiment because their supply of progesterone was exhausted before completion of the study.

## Data analyses

The number of days required to reentrain to a new LD cycle following a phase advance was determined for every animal in each of the experimental conditions, allowing each animal to serve as its own control. Activity data were collected throughout all phases of the experiment as wheel rotations per 10-min interval with VitalView software (Minimitter, Inc.).

Activity onset was measured, as previously described (Goel and Lee, 1995a,b; Jechura et al., 2000, 2003), relative to the onset of the light cue and was defined as at least 40 min of consecutive activity with a minimum of 40 wheel revolutions per 10-min block of activity following a lack of activity of at least 4 h before lights on. The time of activity onset over a period of 4–7 days was averaged and compared to the LD cycle to obtain phase angle of activity onset before phase shifts. Reentrainment was operationally defined as the first day on which the animal displayed a morning phase angle of entrainment within 20 min of the

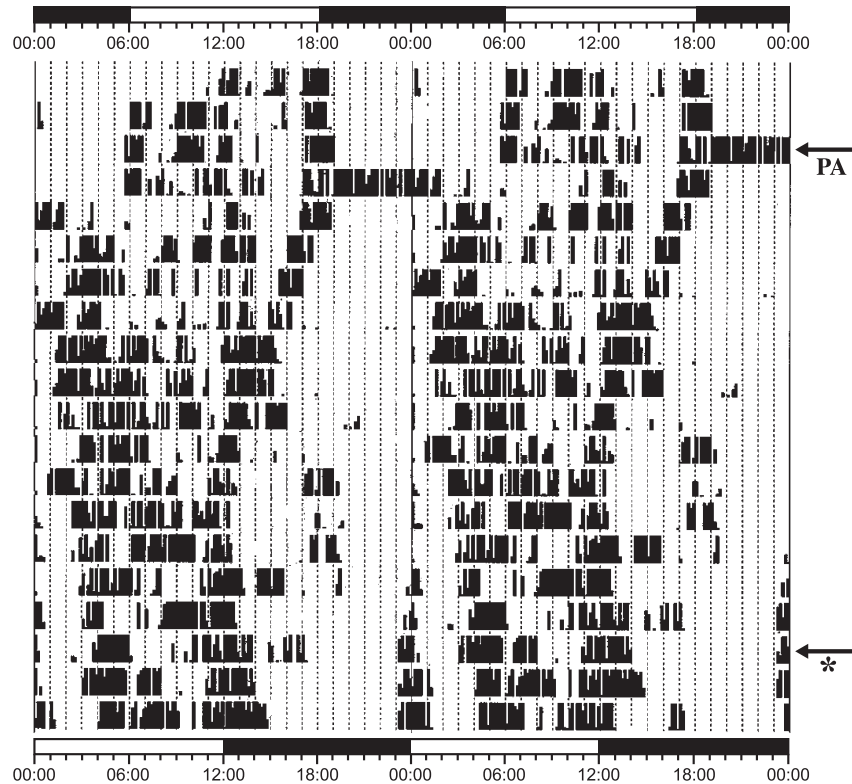


Fig. 1. Double-plotted actogram displaying a typical pattern of activity rhythm reentrainment following a 6-h phase advance of the LD cycle. The light–dark bar at the top of the figure designates the light cycle before the shift, and the bar at the bottom of the figure notes the LD cycle after the shift. “PA” corresponds to the first day of the phase advance and “\*” refers to the day the animal was determined to be completely reentrained to the new light schedule as determined by a return to the original phase angle of activity onset. This animal took 15 days to reentrain.

phase angle before the phase shift for at least three consecutive days (see Fig. 1). All data were analyzed by three scorers, two of which were blind to conditions.

Repeated measures ANOVA and Bonferroni-adjusted post hoc paired *t* test comparisons were used to compare responses to different donor odors in Experiment I, with  $P < 0.05$  considered significant. In subsequent experiments, paired *t* tests were used to compare reentrainment rates following shifts with and without a donor within the same hormonal condition. Subsequently, the control shifts (shifters unexposed to donor odors) were also compared across experiments to determine the reliability of this response across groups (Experiments I–III) and between the same animals in different experiments (Experiments II and IV). Data are presented as means  $\pm$  SEM.

## Results

### Experiment I

Intact females shortened the length of time to reentrain following a 6-h phase advance of the LD cycle only in the presence of an intact female donor compared with phase-shifts while housed alone (post hoc paired  $t = -2.611$ ,  $P < 0.05$ ; Fig. 1). There were no significant

differences in reentrainment rates in the presence of a castrated male, testosterone-treated castrated male, or phase shifting alone. However, the presence of an OVX female as an olfactory cue donor significantly lengthened the amount of time needed to reentrain after a 6-h phase advance compared to reentrainment while alone (post hoc paired  $t = 3.34$ ,  $P < 0.05$ ).

### Experiment II

Intact females responded to an intact female donor by accelerating their reentrainment rate compared to reentrainment alone with only photic zeitgebers (paired  $t = 4.55$ ,  $P < 0.01$ ; Fig. 2). After ovariectomy, there was no significant difference in the length of time to reentrain with a donor compared to reentrainment while alone, or while alone and intact. However, intact females paired with a donor reentrained faster than after OVX while alone (paired  $t = -2.78$ ,  $P < 0.05$ ) or with a donor (paired  $t = -6.74$ ,  $P < 0.01$ ).

### Experiment III

OVX females with EB capsule implants did not display accelerated reentrainment in the presence of a female social cue donor following a 6-h phase advance of the LD cycle

compared to the same type of shift before receiving EB ( $12.33 \pm 1.18$  vs.  $12.4 \pm 1.16$  days, paired  $t = 0.13$ ,  $P = 0.9$ ; Fig. 3). There was also no difference between the OVX females' reentrainment rates while housed alone compared to housing with an intact female social cue donor ( $13.6 \pm 1.07$  vs.  $12.4 \pm 1.16$  days, paired  $t = -1.450$ ,  $P = 0.18$ ).

#### Experiment IV

Following replacement of EB and P with Silastic capsule implants, there was a significantly shorter rate of reentrainment while exposed to olfactory cues ( $24.67 \pm 1.86$  vs.  $17.17 \pm 0.95$  days, paired  $t = 6.38$ ,  $P < 0.01$ ). Note that these were the same animals used in Experiment II, which were unresponsive following ovariectomy. The animals were once again responsive to the accelerating effects of a female olfactory cue donor with the estrogen and progesterone implants.

#### Comparison of control shifts

The rate of reentrainment for animals in Experiments I–IV during reentrainment in the absence of donors differed significantly between treatments ( $F = 8.958$ ,  $df = 4, 28$ ;  $P < 0.001$ ). The control shifts of intact animals in Experiment I, intact animals in Experiment II, OVX animals in Experiment II, and OVX + EB animals in Experiment III did not differ between animals (using Bonferroni-adjusted post hoc comparisons). However, the animals in Experiment IV,

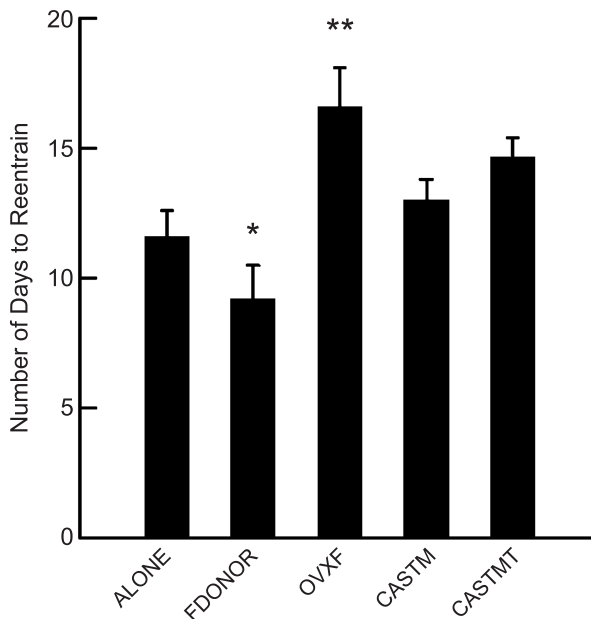


Fig. 2. Length of time for intact females ( $N = 8$ ) to reentrain following a 6-h phase advance of the LD cycle with only photic cues (ALONE) as zeitgebers or with the addition of olfactory cues from an intact female (INT F), OVX female (OVX F), castrated male (CAST M), and T-treated castrated male (CAST M + T). Data are presented as means  $\pm$  SEM. \* $P < 0.05$ , significantly shorter than control (ALONE). \*\* $P < 0.05$ , significantly longer than ALONE.

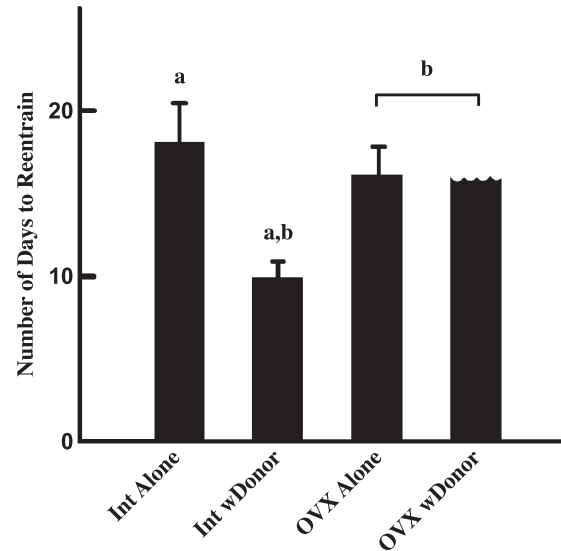


Fig. 3. Length of time to reentrain after a 6-h phase advance of the LD cycle of females ( $N = 8$ ) reentraining alone, with only photic cues (Int Alone), in the presence of a female olfactory cue donor (Int wDonor), and again either alone or with a donor after ovariectomy (OVX Alone; OVX wDonor). Data are presented as means  $\pm$  SEM. Bars represented by the same letters (a and b) are significantly different. Note that at the end of the test of OVX animals with a donor, equipment failure occurred before reentrainment was fully complete for all animals. However, it is clear that donor odors did not hasten reentrainment. Significant difference between intact alone and intact with donor,  $P < 0.01$ ; and between intact with donor and OVX,  $P < 0.05$  and  $P < 0.01$ .

given EB and P capsules, took significantly longer than the controls in Experiment I ( $P < 0.001$ ), OVX + EB implanted animals in Experiment III ( $P < 0.001$ ), and themselves when OVX in Experiment II ( $P < 0.01$ ). However, they did not take longer than themselves in Experiment II when still intact.

#### Discussion

In the first experiment, we report that only odors from an intact female are effective for decreasing the number of days needed to reentrain after a 6-h phase advance. There was no difference in the number of days to reentrain when housed alone or with castrated males and testosterone-treated castrated males, while OVX donors increased the time required to reentrain. Thus, ovarian hormones are necessary for female production of the effective olfactory stimuli. These results are supported by prior experiments in which intact females, but not males, are effective olfactory stimuli donors for phase advances (Goel and Lee, 1995a). The extended length of time required to reentrain in the presence of an OVX donor could be explained by an aversive odor from or the novelty of the OVX females to the experimental animals. This is the first evidence that an odor can have a negative impact on reentrainment rates. Further exploration is needed to determine what types of odors are able to delay

reentrainment and how these odors interfere with the reentrainment process.

By examining the effectiveness of castrated males as olfactory cue donors, we determined that testosterone is not suppressing the males' ability to produce the necessary olfactory cue used by the shifting animal after a 6-h phase advance; females did not accelerate their rate of reentrainment in the presence of castrated males. Previously, we found that testosterone suppresses the males' ability to respond with accelerated reentrainment (Jechura et al., 2003). This indicates that the response and production systems are different in their use of testosterone in the male; responsiveness is actively suppressed by testosterone, but production of an effective odor cue is not reinstated with castration. Thus, the production system in the male degu is unaffected by adult testosterone levels. This is likely due to sexually dimorphic systems responsible for social olfactory cue production, such as anal and flank glands. It should be noted, however, that males are able to produce an effective accelerating olfactory cue for females that are phase delaying, so male cues are effective under certain phase-shifting conditions (Goel and Lee, 1995b).

In the second experiment, we found that OVX females could not accelerate their rate of reentrainment while in the presence of an intact female donor following a 6-h phase advance of the LD cycle. Thus, ovarian hormones are necessary for responsiveness to the accelerating effects of olfactory social cues in females.

The third and fourth experiments reveal that estrogen alone is not sufficient to reinstate the responsiveness of OVX females to olfactory cues used to accelerate reentrainment in the presence of a female donor, but a combination of estrogen and progesterone is effective. However, to make a more definitive claim of the effects of hormones on reentrainment rates with odors, it would be beneficial to examine reentrainment rates both with and without odors in hormone-treated and non-treated animals.

Although a combination of hormones was used, it appears that progesterone is the necessary hormone involved in producing the effective olfactory cue for enhanced reentrainment rates. In fact, post hoc evidence from the two animals that were eliminated from the study because they exhausted their supplies of progesterone from their implants points to the importance of progesterone. The animals that exhausted their progesterone implants did not accelerate reentrainment in the presence of social cue donors during the final phase advance. The remaining animals in the study still had progesterone available in their capsules at the end of the experiment and all responded to the donors. However, a future empirical study of the effects of progesterone alone would be beneficial to conclude that progesterone is the effective hormone in the absence of estrogen.

The current studies also demonstrate variation in rates of reentrainment among similar control ("Alone") conditions between experiments. Animals in Experiment I appear to take less time than animals in other groups, while animals in

Experiment IV appear to take longer. However, control shifts in Experiments I–III did not differ. The same animals were used in Experiments II and IV, and they did not differ between the intact alone shift (II) and the EB + P alone shift (IV). However, the animals in Experiment IV took significantly longer to shift than the intact controls of Experiment I, or the OVX + EB animals of Experiment III, and than themselves after they were OVX in Experiment II.

Similar to humans, degus display variability between individuals in entrained rhythms and rates of recovery after phase shifts (Labyak and Lee, 1997). As mentioned previously, the animals used in these experiments were obtained from an outbred colony of degus, which, unlike inbred strains of rats, hamsters, and mice, maintains individual differences. Because of the expected individual variation and possible variation between groups, each set of experiments was designed with its own control condition. It appears possible that EB + P lengthens the time to reentrain after a phase shift (Experiment IV); however, because they did not differ from themselves as intact animals (Experiment II), these data are not conclusive. Further data need to be collected to verify whether EB + P has a delaying effect. Despite these results, however, it is clear that EB + P treatment allowed animals to respond to the odors of intact females by reentraining 32% faster than without those odors, as was the case for the intact animals.

Odors are an important source of information for most mammals. The ability of rodents and many other species to distinguish conspecifics from non-conspecifics, to differentiate males from females, and to determine whether a female is in estrus or a male has high testosterone levels depends mainly on the ability to use odors as informative signals and to discriminate among subtle differences in odors. Therefore, it is not surprising to learn that odors can influence some aspects of circadian rhythms, as previous data from this laboratory have demonstrated (Goel and Lee, 1995a,b; Governale and Lee, 2001; Jechura et al., 2000, 2003). The ability of odors to accelerate reentrainment is not surprising, given that research in other species, including humans, has shown that the olfactory system can influence circadian rhythms (Grasso and Goel, 2002; Honrado and Mrosovsky, 1989; Pieper and Lobocki, 1991). Sensitivity to entraining effects of odors may be important for female degus during periods of time when the females spend extended periods in their burrows late in pregnancy and for 2 weeks early in lactation (Jesseau, unpublished data). The ability of odors to act as weak zeitgebers (Governale and Lee, 2001) may result in the added effect of altering rates of reentrainment as well as an added signal with light.

These data should promote further research on sex differences in zeitgeber sensitivity and the activational role of gonadal or other hormones on circadian responses. To date, the sex differences in circadian function have been primarily accounted for by prenatal steroid exposure. An olfactory zeitgeber may be somewhat unique because of the sexually dimorphic receptor and anatomical system. However, it may

be the case that other zeitgebers are also filtered through sexually dimorphic receptor systems producing sex-specific sensitivities. It is also possible that the adult circadian mechanism in the suprachiasmatic nucleus is sexually dimorphic or sensitive to steroid hormones, as suggested by common sex differences in free-running rhythms and phase angles of activity onset. Lastly, we should consider the possibility that many weak timing cues may also have additive effects with light during phase shifts and could be used to enhance recovery for desynchronized humans.

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