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Daily Melatonin Injections Affect the Expression of Circadian Rhythmicity in Djungarian Hamsters Kept under a Long-Day Photoperiod

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Key Words. Photoperiodism · Melatonin · Circadian rhythmicity · Seasonal adjustment · Body weight · Reproduction · Molt

Abstract. Djungarian hamsters *(Phodopus sungorus)* kept under a long-day photoperiod (16 h light:8 h dark) were injected with melatonin each day. Hamsters which responded physiologically to this treatment (gonadal regression, molt, body weight loss) phase-advanced onset and extended duration of activity. Hamsters which were physiologically insensitive to melatonin injections did not exhibit such changes in activity pattern and often failed to entrain to the light:dark cycle. Hamsters given saline injections did not alter activity or exhibit gonadal regression, weight loss and molt to the winter pelt. Melatonin-sensitive hamsters compressed duration of activity when they became physiologically refractory to the melatonin treatment (weeks 27–29). At the same time, melatonin-insensitive hamsters became entrained to the light:dark cycle. Thus, daily melatonin injections induce short-day-like adjustments in activity under a long-day photoperiod. These changes in activity are correlated with melatonin-induced gonadal regression, weight loss and molt.

The photoperiodic adjustment in the Djungarian hamster, *Phodopus sungorus sungorus,* has been extensively studied in the past 15 years. When kept under a short-day photoperiod of less than 13 h of light per day [11, 19], this hamster exhibits a syndrome of winter adjustments including body weight loss, molt to a white winter pelt, reproductive regression and an increase in thermoregulatory heat production [16, 18, 31]. Such a photoperiodically regulated syndrome depends on the precise determination of daylength and requires a functional circadian system entrained to the light:dark cycle [12]. Information about daylength is coded by the nocturnal pulse of melatonin, a hormone of the pineal gland [15, 17]. Melatonin is produced in a rhythmic fashion in that levels are high during night and decline prior to lights on [15]. This daily pattern in melatonin production and secretion is driven by the circadian system [10, 21, 35]. The duration of the nocturnal melatonin pulse appears to be the critical attribute necessary for the induction of short-day adjustments [6], although specifics on how duration is measured are less clear. One current hypothesis assumes a period of sensitivity for melatonin which presumably is under the control of the circadian system [32, see ref. 30 for review]. According to this hypothesis, melatonin injections given in the afternoon phase shift a sensitivity rhythm (presumably via the circadian system) so that its coincidence with the endogenous, nocturnal melatonin pulse results in a short-day adjustment under a long-day photocycle. An assumption of this hypothesis is that melatonin can phase-shift the circadian rhythmicity. This assumption has not been experimentally verified.

Although there is ample evidence that the pineal gland is not important in the generation of mammalian circadian rhythms [2], melatonin does affect the circadian function. For example, melatonin injections can entrain the activity onset in free-running laboratory rats [29]. Weaker evidence is also available that melatonin might alter the duration of wheel-running activity in the rat [4]. Finally, melatonin alters the mammalian hormonal state which may in turn influence the circadian rhythmicity [see ref. 34 for a review].

In this study, we establish that melatonin injections affect the expression of circadian rhythmicity in the Djungarian hamster. We also establish that spontaneous refractoriness to extended melatonin administration applies for these melatonin-induced changes in activity.

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Material and Methods

Forty-one adult Djungarian hamsters (70–150 days) were bred and raised under long-day conditions (16 h light:8 h dark; lights on at 4.30 EST). The animals were derived from a breeding colony originally obtained from Dr. Bruce Goldman of the Worcester Foundation for Experimental Biology. They were randomly assigned to one of two treatments. Twenty-three hamsters (13 females and 10 males) were injected daily with 0.1 ml of 1% ethanol-saline solution containing 25 µg melatonin (Sigma, St. Louis, Mo.). The remaining hamsters (8 females, 10 males) were injected with ethanol-saline vehicle. Injections were given at 12 h after lights on (16.15–16.45 h). Such melatonin injections have been shown to be effective at inducing physiological short-day adjustments under a long-day photoperiod [20]. Body weight and fur color [after ref. 13] were assessed at weekly intervals, and testis length in males was measured by external palpation every other week.

During activity measurements individual hamsters were housed in a polypropylene cage (24 cm × 35 cm × 21 cm), which was equipped with a 27-cm-diameter wheel. To facilitate hamster running, wheels were lined with fine wire mesh. Wheel-running activity was recorded on a 20-channel event recorder (Esterline Angus, Indianapolis, Ind.). At week 10, activity was recorded for 16 days on 10 saline-injected and 10 melatonin-injected hamsters which already showed a response to the melatonin treatment, as indicated by gonadal regression, body weight loss and molt. After week 19, activity was continuously recorded on all of the melatonin-injected hamsters. Daily injections ended at week 32, but activity measurements continued for another 3 weeks.

Daily activity records were pasted beneath each other, photoreduced and double-plotted to facilitate the visualization of avtivity patterns. Onset and offset of activity were determined with the following qualification. Onset of activity was designated as the first activity bout lasting more than 5 min. Activity bouts shorter than 5 min often followed the injection and were thus ignored in our calculations. Duration of wheel-running activity (α) was defined as the time interval between onset and offset of activity. Daily onset and α were averaged for hamsters between week 10 and 12 and in weekly intervals for weeks 19–35. The phase of activity onset was calculated in reference to lights off. The phase angle (ψ, hours) is positive if activity onset preceded lights off and negative if it followed lights off.

Results are expressed as means ± SEM. Analysis of variance was performed to test for differences in continuously varying traits. When a significant treatment effect was found, comparisons between independent means were made using the error term from the analysis of variance and the t distribution. A paired sample t test was performed for dependent variables. Regressions were calculated by the method of least-square deviation.

Results

During the first 10 weeks of melatonin injections, 12 of the 23 hamsters (6 males, 6 females) lost body weight (–3.1 ± 1.0 g; $p < 0.01$ relative to initial values; fig. 1a). Further, these hamsters started to molt at week 7 and all exhibited a molt by week 15. Testicular regression was evident by week 9 in the 6 male hamsters (9.7 ± 0.4 mm; relative to an initial value of 12.5 ± 0.2, $p < 0.01$). One of the melatonin-injected female hamsters started a partial molt at week 20, but molted back to the summer pelt 6 weeks later. No consistent trends in body weight were observed in this individual. Due to the late timing of the response, this individual was excluded from further data analysis. The remaining 10 melatonin-injected hamsters (4 males, 6 females) gained weight during the first 10 weeks of the study (3.3 ± 1.0 g; relative to inital weights, $p < 0.02$; fig. 1b), remained reproductively competent (testis length at week 9 of the 4 male ham-

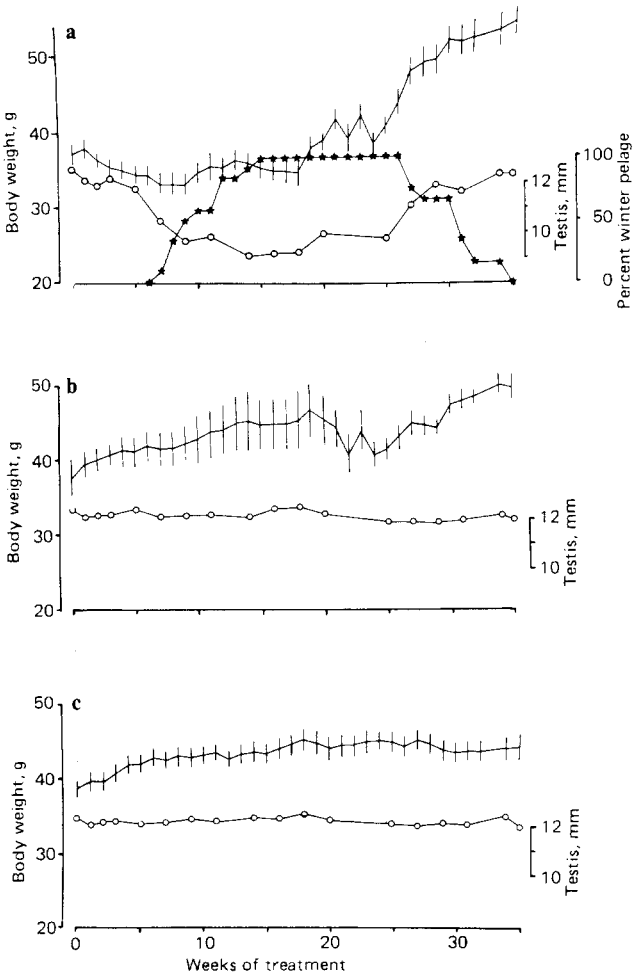

Fig. 1. Mean (± SEM) change in body weight (no symbols), testis length (open circles) and molt to the winter pelt (stars) in hamsters responding to daily, afternoon melatonin injections **(a),** hamsters not responding to these melatonin injections **(b),** and hamsters given saline injections **(c).** No hamster molted in groups **b** and **c.** Hamsters were maintained on a long-day photoperiod (16 h light:8 h dark; lights on 04.30 h) and were injected each day for 32 weeks at 16.15–16.45 h with either 25 µg melatonin or saline.

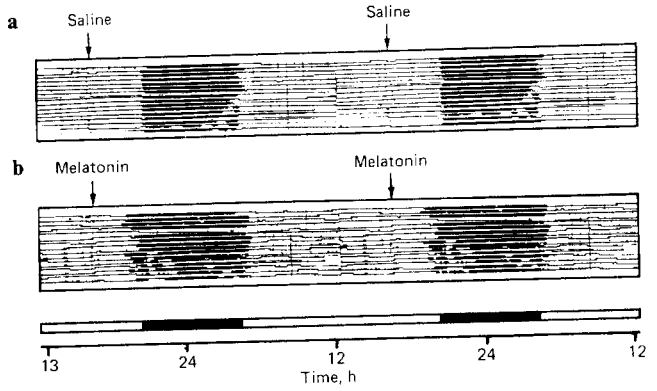

Fig. 2. Wheel-running activity of a saline-injected **(a)** and melatonin-injected **(b)** hamster. After 10 weeks of injections, activity was recorded for 16 days. The black bars beneath the activity records represent the 8 h of darkness per day. Arrows indicate the time of injection. To facilitate the visualization of the data, the activity records are double-plotted.

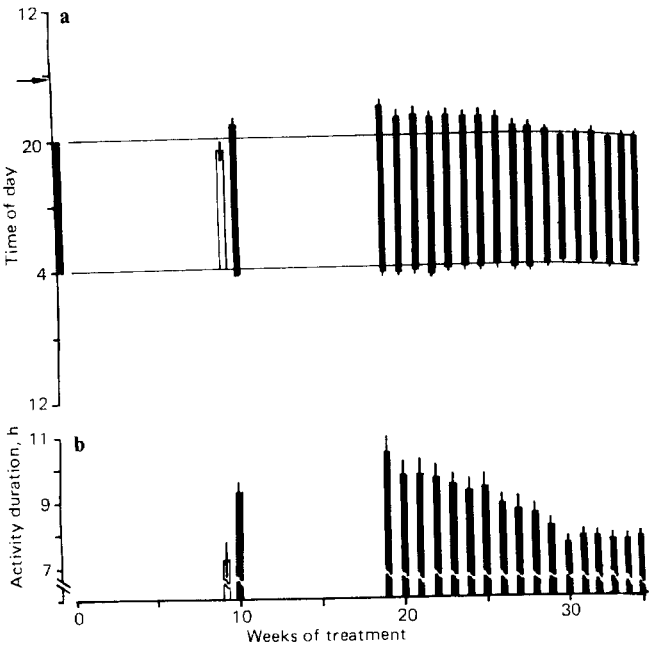

Fig. 4. Mean (±SEM) activity onset and offset for hamsters which responded to melatonin injections (solid bars in **a**). For comparison, week 10 data for saline-injected hamsters are also given (open bars). The arrow indicates the time of injection. Mean (±SEM) duration of activity (α) for these hamsters appears in **b**. Note the compression of activity duration during the latter weeks of the study.

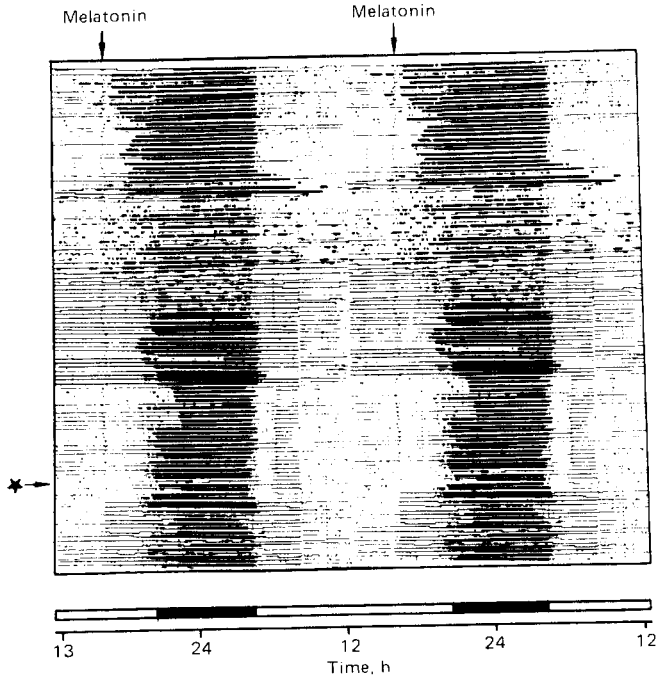

Fig. 3. Wheel-running activity (from week 19 through week 35) of a hamster which responded to the daily melatonin injections. Injections ended at week 32 (star). Note the compression in activity duration (α) resulting from a gradual phase delay in activity onset. See figure 2 caption for details.

sters = 12.5 ± 0.3 mm; $p < 0.01$ relative to melatonin-sensitive hamsters) and did not molt to a winter pelt. They maintained a long-day physiological state throughout the 35-week study. The saline-injected hamsters also gained weight (5.0 ± 1.1 g; week 10 versus initial weights, $p < 0.01$; fig. 1c). No saline-injected hamsters exhibited a molt to the winter pelt, testicular regression or a consistent weight loss during the experiment.

Hamsters which responded to melatonin started to gain body weight at week 19. Although a consistent weight gain eventually occurred in each individual, mean weight for the group fluctuated between week 19 and 25. This variability might be due to altered housing conditions, since most hamsters exhibited fluctuations in body weight following access to running wheels. Gonadal recrudescence was observed in 2 of the male hamsters at week 20 and in the remaining 4 hamsters at week 27. By week 29, average testis length was similar to that measured at the beginning of the study (fig. 1a). At week 27, the first hamster molted back to a summer pelt, and by week 32 all but 2 hamsters had molted to the gray-brown pelt (fig. 1a).

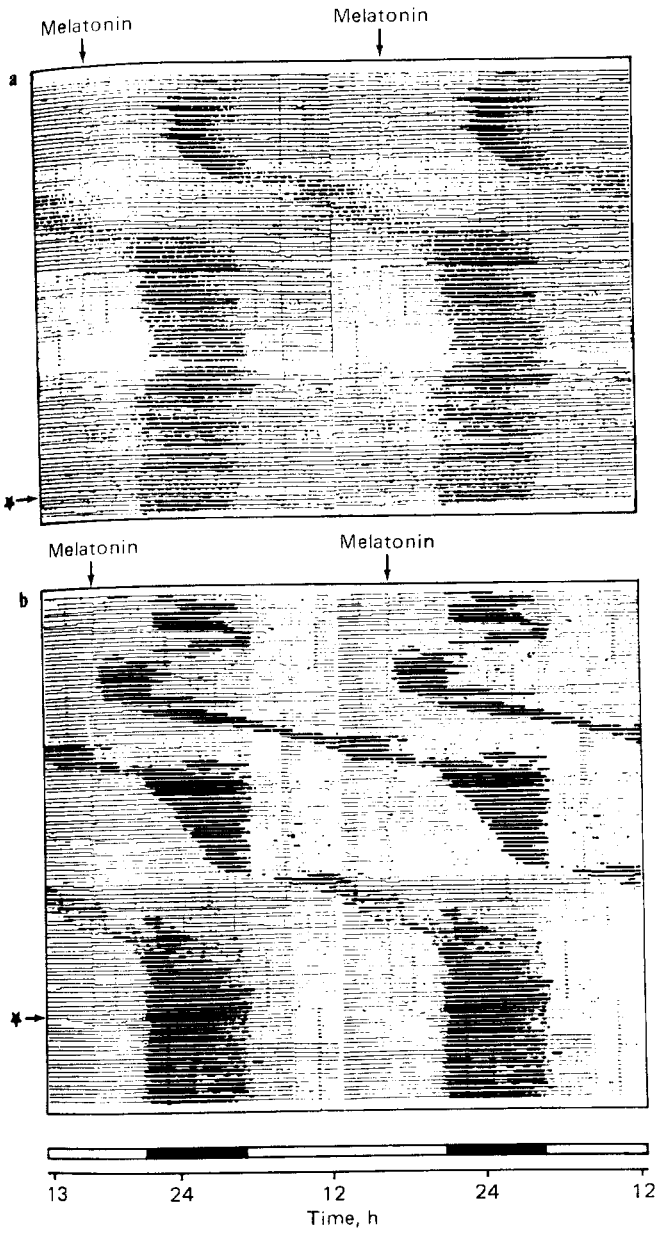

Fig. 5. (a, b) Wheel-running activity (from week 19 through week 35) for 2 hamsters which did not exhibit weight loss, a molt or gonadal regression following melatonin injections. Note the periods of free-running activity and lack of proper entrainment to the light:dark cycle. Daily injections ended on week 32 (star). See figure 2 caption for additional details.

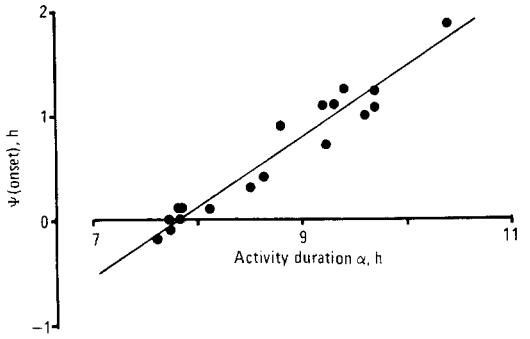

Fig. 6. Correlation between phase angle (ψ) of activity onset relative to lights off and activity duration (α). A positive phase angle indicates that activity onset occurred prior to lights off while a negative value indicates that activity onset followed lights off. Each black dot represents a weekly mean in wheel-running activity of hamsters which responded to the melatonin injections. The correlation coefficient is significant ($r = 0.97$; $p < 0.01$). The slope is 0.66.

In contrast to saline-injected controls, melatonin-sensitive hamsters at week 10–12 started to use the running wheels well before lights off [ψ(onset): melatonin = +0.7 ± 0.3 h, saline = −0.8 ± 0.5 h; $p < 0.02$; see fig. 2 for representative data]. Additionally, duration of wheel-running activity was considerable longer in melatonin-sensitive hamsters (α: melatonin = 9.2 ± 0.3 h, saline = 7.2 ± 0.6 h; $p < 0.01$; fig. 2). By week 19, anticipation of lights off was even more pronounced in melatonin-sensitive hamsters [ψ(onset) = +1.9 ± 0.5 h], resulting in a prolonged activity duration (α = 10.4 ± 0.5 h; fig. 3, 4). Following week 19, onset of activity gradually shifted to lights off in these hamsters, associated with a compression of α. By week 30, activity rhythms were similar [ψ(onset) = +0.1 ± 0.2 h, α = 7.8 ± 0.2 h; fig. 3, 4) to those of saline-injected controls at week 10.

Hamsters which did not undergo gonadal regression, weight loss or molt following melatonin treatment often exhibited free-running activity (fig. 5). In some of these animals, entrainment (or masking by the photophase) of activity offset was observed (fig. 5b). Episodes of free-running activity occurred in all but 2 of the hamsters. One of these two hamsters entrained to the light:dark cycle but did not exhibit a decompressed α characteristic of melatonin-sensitive individuals. The second hamster lacked a clear activity pattern.

With continued melatonin administration, melatonin-insensitive hamsters eventually entrained to the light:dark cycle. By the last week of melatonin injections (week 32), 4 of 7 melatonin-insensitive hamsters exhibited an activity pattern similar [ψ(onset) = 0.5 ± 0.1 h after lights off, α = 7.4 ± 0.4] to that previously observed in the saline-injected hamsters (week 10; fig. 4). The remaining 3 hamsters started to run before lights off [ψ(onset) = +3.3 ± 0.5 h] and exhibited a long activity period (α = 11.2 ± 0.5). Three weeks after the end of the melatonin injections, 9 of the 10 nonresponsive hamsters were entrained to the light:dark cycle [ψ(onset) = −0.4 ± 0.3 h; α = 7.6 ± 0.4 h].

Discussion

Daily melatonin injections given in the afternoon extend the duration of activity, resulting in an activity pattern which is similar to that seen under a short-day photoperiod [25, 26]. Thus, melatonin's effectiveness at eliciting short-day adjustments under a long-day photoperiod is not restricted to physiological traits, such as gonadal regression or thermoregulatory enhancement [17, 18]. In fact, the melatonin-induced alteration of activity is correlated with the ability of this hormone to induce physiological short-day adjustments since only hamsters which exhibited short-day characteristics in activity underwent short-day-like adjustments in reproduction and thermoregulation. Further, the timing of spontaneous refractoriness to melatonin is the same for activity and the physiological traits. After 27–29 weeks of melatonin administration, compression of α and a return to the summer physiological state (i.e. gonadal recrudescence and molt to the summer pelt) occurred simultaneously. No sex difference in the responsiveness to melatonin administration or in the timing of refractoriness was found.

The extended duration of activity in melatonin-sensitive hamsters is mainly due to a phase advance in activity onset (fig. 6). In order to maintain the positive phase relationship between onset of activity and lights off, melatonin injections must override the phase-delaying effect of the light experienced in the early subjective night [26] by a strong phase-advancing action. Whether melatonin's phase-advancing action depends on the timing of the injection, as demonstrated for other physiological adjustments [20], has yet to be tested. However, the correlation between the phase-advancing action and melatonin's ability to induce short-day physiological adjustments supports such a hypothesis.

The circadian basis by which melatonin might induce these short-day-like adjustments is not understood. The observed phase advance might indicate a melatonin-induced shortening of τ [1, 22, 37]. Alternatively, melatonin injections might have an effect similar to darkness, thus overriding the phase-delaying effect of light experienced in the early subjective night. Both these alternatives assume an effect of daily melatonin injections on circadian rhythmicity. At present, there is a controversy as to whether melatonin affects the mammalian circadian rhythmicity. Perhaps the strongest evidence for a melatonin effect on circadian function comes from the observation that rats [28] and hamsters [14] re-entrain faster to a changed light:dark cycle if they are pinealectomized. Furthermore, Redman et al. [29] reported an entraining effect of daily melatonin injections in rats under constant darkness. This effect depends upon an intact suprachiasmatic nucleus [7]. Melatonin might also alter the duration of wheel-running activity [4]. However, the studies of Cheung and McCormic [8] and Quay [27] failed to demonstrate that melatonin affects the circadian rhythmicity. Finally, Aschoff et al. [2] have pointed out that differences in rate of re-entrainment might be due to a masking effect of melatonin. Such a possibility cannot be dismissed as an explanation for the results presented here.

Further, melatonin's action might not be a direct one, but the result of an altered hormonal state following melatonin-induced physiological short-day adjustment, such as the hormonal changes associated with gonadal regression. Such hormonally mediated effects seem possible, since a number of steroid [3, 9, 23, 33, 34] and nonsteroid hormones [5, 24, 36] can affect the expression of circadian rhythmicity, and melatonin's potential to alter the neuroendocrine-gonadal activity is well established. At present, these fundamental questions regarding the functional aspects of melatonin's action on the expression of circadian rhythmicity cannot be conclusively answered.

Melatonin injections do not induce physiological adjustments in some hamsters (fig. 1b), and these individuals also fail to phase-shift activity onset into the photophase. However, melatonin does affect the activity pattern of these hamsters in that they are often incapable of entraining to the light:dark cycle (fig. 5). Such a melatonin effect has not been reported previously. This effect ceases at about weeks 27–29 (fig. 5b). As mentioned earlier, it is at this time that the melatonin-sensitive hamsters became refractory to continued melatonin treatment. This temporal similarity between the melatonin-sensitive and -insensitive groups indicates that the timing of refractoriness is not dependent upon the prior physiological state. A corollary to this idea is that the previous hormone state per se does not influence the occurrence of refractoriness in this species. These results imply that the timing mechanism controlling the onset of refractoriness may be independent of the mechanism responsible for photoinduction in this species.

Since the exogenous melatonin and endogenous melatonin pulse are critical for short-day-like adjustments [6, 20, 32], there are at least two possibilities to explain a physiological insensitivity to melatonin: (1) the exogenous melatonin injection at this time point is ineffective, or (2) the endogenous melatonin rhythm might be altered. With regard to the latter possibility, we reported in another study [25] that the melatonin-generating system is deficient in short-day-insensitive hamsters. Further, this inability to generate a short-day melatonin pulse has a circadian basis. Short-day-insensitive hamsters exhibit a different phase response curve under constant darkness than responsive hamsters. Additionally, short-day-insensitive hamsters have a longer free-running period in constant darkness, and rarely exhibit a split in their activity rhythm under constant light [26]. However, we have not examined whether hamsters physiologically insensitive to a short-day photoperiod are the same individuals which are insensitive to melatonin injections. The possibility that insensitivity to both melatonin and short days might have a common circadian basis is currently under investigation.

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