

Seasonal Variations in Circadian Rhythms of Plasma Melatonin in Ruin Lizards

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We examined melatonin profiles of ruin lizards in different seasons (spring, summer, and autumn) under light: dark (LD) and concomitant responses when transferred to continuous darkness (DD) to determine the degree to which previously reported seasonally dependent effects of pinealectomy on locomotor behavior are related to melatonin secretion. The amplitude of the melatonin rhythm and the amount of melatonin produced over 24 h varied with season. In spring, the amount of melatonin produced was greatest and the amplitude 4–5 times that found in summer or autumn. The degree of self-sustainment of the melatonin rhythm when transferred to DD also varied with season. In DD, melatonin levels remained high but did not exhibit circadian variation in spring. In summer, the melatonin profile persisted virtually unchanged in DD, showing the existence of a circadian rhythm. Finally, in the fall there was no circadian variation in DD and levels remained low. These responses correspond closely to previously reported effects of pinealectomy on locomotor behavior where there is little or no effect of pinealectomy in spring or fall but a profound alteration of locomotor behavior in summer. These results suggest that the seasonally dependent effects of pinealectomy on locomotor behavior in ruin lizards are related to a seasonally mediated change in the degree of self-sustainment of some component of the circadian pace-making system of which melatonin plays some role. © 2002 Elsevier Science (USA)

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INTRODUCTION

In most vertebrates melatonin is synthesized mainly in the pineal gland and rapidly secreted into the blood. Whether measured in the pineal or the blood, melatonin oscillates with a daily rhythm with levels high at night and low during the day (Reiter, 1977; Arendt, 1987; Underwood, 1992). In some birds and lizards the isolated pineal cultured *in vitro* synthesizes melatonin with a circadian rhythm, which persists for several cycles in constant conditions, demonstrating the existence of circadian oscillators in the pineal that are coupled to melatonin synthesis (Binkley *et al.*, 1978; Deguchi, 1979; Takahashi *et al.*, 1980; Murakami *et al.*, 1994; Tosini *et al.*, 2000). Additional studies in the Iguanid lizard *Anolis carolinensis* have demonstrated that 24-h cycles of both light and temperature can entrain the pineal melatonin rhythm and that differences in length of daily photoperiod or thermoperiod affect the phase, amplitude and duration of this rhythm (Underwood, 1985; Underwood and Calaban, 1987). Hence, the current ambient lighting and temperature conditions are readily translated into an internal cue in the form of the pineal melatonin rhythm. This cue can be used to regulate both the daily and annual physiology of lizards (Underwood, 1985).

In our model animal, the ruin lizard *Podarcis sicula*, seasonal differences in the locomotor activity pattern of intact animals kept in constant conditions were found to be associated with systematic differences in both the freerunning period (τ) of locomotor rhythms and the length of circadian activity (α) (Foà *et al.*, 1994). The bimodal locomotor pattern expressed by ruin lizards in summer is typically associated with a short τ and a long α , whereas the unimodal pattern expressed in spring and autumn is typically associated with a long τ and short α (Foà *et al.*, 1994). Melatonin

and the pineal play a central role in this seasonal reorganization of the circadian system (Innocenti *et al.*, 1994, 1996). Either pinealectomy or chronic administration of exogenous melatonin (implants) induces an immediate transition from the typical circadian locomotor pattern of summer (bimodal pattern, short τ and long α) to the typical circadian locomotor pattern of spring or autumn (unimodal pattern, long τ and short α) (Foà *et al.*, 1992b; Innocenti *et al.*, 1994). Further experiments showed the existence of marked seasonal variations in the behavioral effects of pinealectomy in ruin lizards (Innocenti *et al.*, 1996). In constant temperature and darkness (DD), changes in τ in response to pinealectomy were significantly greater in summer than in other seasons. Similarly, α changed significantly in response to pinealectomy only in spring and summer. Again, while pinealectomy was effective in altering the locomotor rhythms of all lizards tested in summer, the same surgery left locomotor rhythmicity of many lizards tested in autumn and winter completely undisturbed. In summer, ruin lizards have robust circadian rhythms of plasma melatonin that become abolished in response to either pinealectomy or melatonin implants (Foà *et al.*, 1992a,b). The fact that in summer pinealectomy affects both locomotor behavior and suppresses plasma melatonin rhythms supports the hypothesis that the behavioral effects of pinealectomy are due to the withdrawal of rhythmic changes in plasma melatonin levels. If the hypothesis above is correct then the weak or absent behavioral effects of pinealectomy observed in winter, spring and autumn could be due to absence of a rhythmic production of melatonin during those seasons.

The present investigation was aimed at determining if circadian rhythms of plasma melatonin are present in other seasons, and if there are seasonal variations in the self-sustaining properties of the melatonin rhythms when the lizards are placed in constant darkness. For this purpose, 24-h plasma melatonin profiles of ruin lizards maintained at constant temperature (29°C) in light:dark (LD) and DD were examined in different seasons.

MATERIALS AND METHODS

Animals

Ruin lizards (*Podarcis sicula*, De Betta 1857; adult male only, 6.5- to 8-cm snout vent length) were collected in April 1997 from the area of Ferrara. After

capture, lizards ($n = 39$) were transported to the lab, placed in groups of 4–5 individuals inside plastic containers (43 × 26 × 15 cm) and kept in a vivarium under natural photoperiodic conditions. Approximately, 65 h before blood sampling, the containers were moved to environmental chambers kept at constant temperature (29 ± 0.5°C) and subjected to either a light-dark (LD) cycle roughly corresponding to the natural photoperiod from the same season or to DD. In the chambers, lighting was provided by white fluorescent lamps with an intensity of 900 lx at the level of the head. Food (*Tenebrio molitor* larvae) and water were supplied twice a week. After each experiment the containers were brought back to the vivarium with natural lighting conditions until the next experiment.

Blood Sampling

Blood samples were taken from the lizards every two hours over a 24-h period. Each individual lizard was sampled at 6-hour intervals in a 24-h period and the median sample size per time point was 13 individuals. Each group of lizards was sampled at the same time of day during all tests. For the DD tests, the onset of the DD coincided with the light-to-dark transition of the LD cycle. Each test in DD started at 0800 on the third day after transfer to DD. In DD and during dark phase of the LD cycles, blood was collected with the aid of a weak red light (50 mW/m²) from a fiber-optic light source. Sampling was accomplished by puncturing the infra-orbital sinus with the unpolished end of a 100 μ l ammonium heparinized capillary tube (1.4 mm o.d., Drummond Scientific Company, Broomall, Pennsylvania, USA), and drawing 90–260 μ l of blood. Samples were immediately placed into a 1.5 ml microfuge tube and centrifuged for 12 min at 4000 rpm. Plasma was then aspirated and stored at – 80°C until assayed.

Experimental Design

The first sampling test in DD started in spring (May 21). Tests in DD were repeated in summer (August 06), and autumn (December 17) on the same lizards. Also control tests in LD were repeated at three different seasons: spring (May 07), summer (July 23), and autumn (December 03). In spring and summer, lizards were exposed to 14:10 h LD cycle, while in autumn lizards were exposed to 10:14 h LD cycle. These photoperiods were roughly comparable to natural photoperiods in the respective seasons.

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