

RAPID COMMUNICATION

Occlusion of the Parietal Eye Induces a Transient Wavelength-Dependent Shift in Lizard Thermoregulatory Set Points

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ABSTRACT Thermoregulatory set points—i.e., the body temperatures at which heat-seeking or cooling behavior are initiated—of the lacertid lizard *Podarcis muralis* were measured by infrared thermography before and after covering the parietal eye with light filters with different cut-off points. The results show that shielding the parietal eye results in a transient alteration of thermoregulatory set points; this effect is wavelength-dependent. Mean heating rates, bask and forage durations were not affected by the shielding of the parietal eye with any of the filters used. © 1994 Wiley-Liss, Inc.

The parietal eye of lizards is a photoreceptive structure located on the dorsal surface of the head. Electrophysiological studies have shown that the parietal eye not only responds to illumination, but is also capable of responding differentially to light of different wavelengths (Engbretson, '92; Solessio and Engbretson, '93). It appears that the parietal eye can be involved in a number of processes (e.g., Underwood, '81; Ellis-Quinn and Simon, '91) including thermoregulatory behavior (Ralph et al., '79; Firth and Turner, '82; Phillips and Howes, '88).

Many lizard species are able to maintain their body temperatures (T_b) within a narrow range during activity by behavioral and to a lesser extent by physiological adjustments in relation to the thermal characteristics of their environment (Avery, '82). The neural control of thermoregulatory behavior in these animals is believed to involve two classes of hypothalamic temperature sensitive receptors whose properties and states determine upper and lower 'set points' which define the T_b at which heat-seeking or cooling behavior are initiated (Berk and Heath, '75; Barber and Crawford, '77). In small heliothermic lizard species which thermoregulate primarily by shuttling between microenvironments with different levels of incident solar radiation, the T_b s at which behavior changes can be readily measured. Infrared thermography is particularly appropriate for such studies, because it is non-invasive (Jones and Avery, '89).

There have been many investigations of ways in which the parietal eye can influence the thermoregulatory behavior of lizards (see references

above), but none of these has considered the effects that selective light occlusion of this photoreceptor can produce. The study reported here investigates the effects that different selective light occlusions of the parietal eye produce on the thermoregulatory behavior and set points in a lacertid lizard.

MATERIALS AND METHODS

The species studied was the wall lizard *Podarcis muralis*, which is a small- to medium-sized lacertid (adults usually have a body mass within the range 5–10 g) with a very widespread distribution in central and southern Europe. The individuals used here were collected in Florence (Italy) during the late spring 1992.

Experimental lizards ($N = 5$) were then moved to Bristol (June 3, 1992) and maintained in a laboratory at about 20°C with natural illumination in cages measuring 90 × 40 × 30 cm. For experiments they were housed singly in an open-topped, wooden-floored enclosure measuring 2 × 1.5 m, containing a secure refuge, water and some grass turf and further diversified by the presence of a number of 5 × 5 × 5 cm wooden blocks (Avery, '85). Heat for thermoregulation was supplied from a 60 W tungsten reflector bulb held 20 cm above the floor of the arena, and shone through a metal

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funnel so that only a small pool of heat and light, about 10 cm in diameter, was produced on the floor; this was called the 'basking spot.' The bulb was switched on for 8 hr/day. While the bulb was switched on a lizard usually alternated periods of basking at the basking spot with periods of movement about the cage.

Temperatures of the dorsal surface of the body of basking lizards (T_{surface}) were determined using a pyroelectric vidicon camera as described by Avery and D'Eath ('86). Methods for determining the sensitivity and accuracy of this equipment, and for calibration so that it can be used as a radiation thermometer, are given by Jones and Avery ('89). The T_{surface} recorded when a lizard appeared at the basking spot is termed the lower set point. Surface temperatures were subsequently recorded at 30-sec intervals and finally at the moment when the animal moved off having finished basking. This temperature was termed the upper set point (see Jones and Avery, '89, for a more detailed rationale for this terminology). Previous investigations (Tosini, '93; Tosini and Avery, '93) have shown that in small lizard species the use to T_{surface} may represent a good estimate of hypothalamic temperature.

A series of 10 lower and 10 upper thermoregulatory set points were then recorded in each of the experimental lizards for 1 day before and for 5 days after the parietal eye had been covered with wavelength-selective gelatin filters. Three of these were high wavelength band pass filters with a cut-off points at 480, 540, and 600 nm. A fourth filter allowing >90% transmission at all visible wavelengths acted as control (see Figure 1 for the transmission spectra of the filters used).

In addition to the thermoregulatory set points we also measured the bask duration, the subsequent forage duration, and the heating rate for each of the basking events.

RESULTS

No differences were found in the set point values between individuals in any experimental conditions (one-way ANOVAs, $P > 0.1$, in all cases) and so the data were combined for subsequent analysis. Covering the parietal eye with filters that allowed full light transmission (control filter) or the transmission of light of wavelength longer than 480 nm did not have any effect on the daily means of either set points (one-way ANOVAs, $P > 0.1$, Figs. 2a and b). Covering the parietal eye with filters that allowed light transmission only above 540 nm or 600 nm, however,

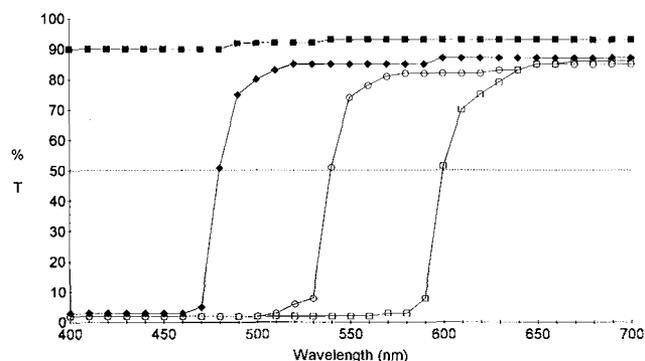


Fig. 1. Transmission (in %) of the four filters used in the wavelength range 400–700 nm recorded with a Pye Unicam (SP8-200) spectrophotometer. (◆) cut-off point at 480 nm; (○) cut-off point at 540 nm; (□) cut-off point at 600 nm; (■) control filter.

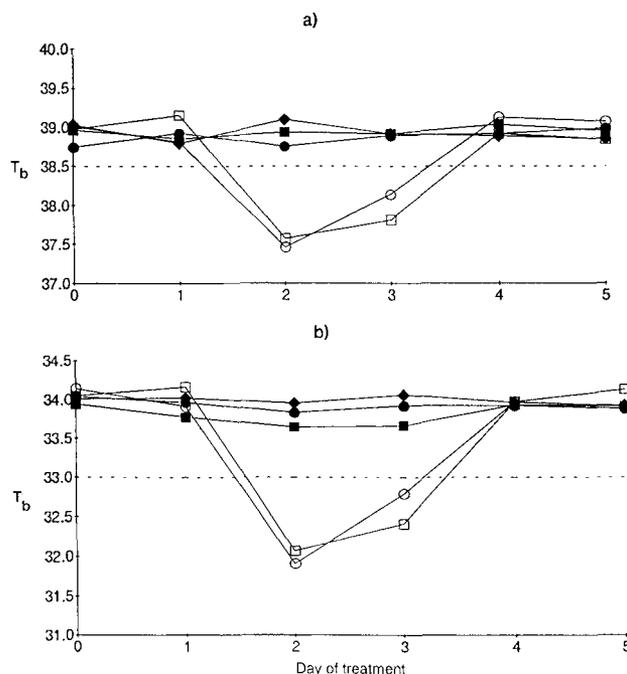


Fig. 2. Overall daily mean values of upper (a) and lower (b) set points before (day 0) and during 5 days during which the parietal eye was covered with filters with different cut-off points. (●) untreated animals; (■) control filter; (◆) light > 480 nm; (○) light > 540 nm; (□) light > 600 nm. Means above the dotted lines are significantly different from means below the dotted lines (T -methods tests, $P = 0.05$). Means above or below the dotted lines do not differ (one-way ANOVAs, $P > 0.1$).

resulted in significant changes in means of both set points (one-way ANOVAs, $P < 0.05$). These changes consisted in a significant reduction in mean upper and lower set point values during the second and the third days after the occlusion (T-method tests, $P = 0.05$; Figs. 2a and b).

Other measured thermoregulatory variables—mean bask duration, mean forage duration, and heating rate—did not show any differences either in respect to days or to treatments (one-way ANOVAs, $P > 0.1$ in all cases).

DISCUSSION

The results show that the parietal eye has a wavelength-dependent effect in the regulation of thermoregulatory set points in *P. muralis*. This effect consists of a significant transient downward shift of both set points (1–2°C). The time lags suggest that the effects are mediated by hormonal rather than neural mechanisms, and probably involve the hormone melatonin which has a thermoregulatory function in most vertebrates including lizards (Gern et al., '86; Rismiller and Heldmaier, '87; Skinner, '91). Plasma melatonin levels in lizards are known to be altered by parietectomy (Firth and Kennaway, '80). The transitory nature of the effect reported here shows that compensation can occur, although the mechanisms are currently unknown.

To our knowledge this is the first time that the electrophysiological results concerning the photosensitivity of this structure recorded by some authors (review Engbretson, '92; see also Solessio and Engbretson, '93) have been associated with a functional role in whole animal performances. The data here presented are consistent with these studies showing that light of wavelengths in the range 480–540 nm are actually important for the functioning of this photoreceptive structure. Based on our data it is plausible to attribute to the parietal eye a potential role as dawn/dusk detector (Solessio and Engbretson, '93) in order to detect the beginning and the end of the daily photophase. Such information could be successively used by the 'thermoregulatory central mechanisms' to determine the activity temperature range, which has been shown to be affected by the photoperiod (Rismiller and Heldmaier, '87). Nevertheless, our data also show that the lack of photic information from the parietal eye can be compensated for and therefore suggest that this organ is not the only photoreceptive structure involved in the regulation of thermoregulatory processes.

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