

Dermal Photoreceptors Regulate Basking Behavior in the Lizard *Podarcis muralis*

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TOSINI, G. AND R. A. AVERY. *Dermal photoreceptors regulate basking behavior in the lizard Podarcis muralis*. *PHYSIOL BEHAV* 59(1) 195–198, 1996.—There is evidence that dermal photic responsiveness can be found in a wide range of animals. Behavioral responses to dermal stimulation by light have been observed in pigeon squabs and new-born rats, and more recently in a sea snake. Here we report that painting the dorsal surface of the lizard (*Podarcis muralis*) with opaque black paint impairs the animal's ability to position itself beneath a light source containing negligible heat. Experiments using light of different spectra and intensities show that the effect is due to light of wavelengths shorter than 600 nm and of intensity higher than 2.5 mW cm⁻². These experiments demonstrate for the first time that overt behavior in a terrestrial vertebrate can be mediated by a dermal light sense.

Photic response	Nonvisual photoreception	Extra-retinal photoreception
Behavioral thermoregulation	Lizard	<i>Podarcis muralis</i>

THERE is evidence for dermal light responsiveness in a wide range of invertebrates and vertebrates. Dermal light receptors are differentiated from heat receptors because they respond exclusively to the visible electromagnetic spectrum (400–700 nm). While dermal photoreceptors are distinguished by the fact that they do not exist as part of, or in direct association, with the brain, the anatomical basis for dermal photoreception remains unclear. Dermal photic responsiveness has been studied primarily using nonbehavioral (e.g., electrophysiological) measures (1,5,16). Amongst vertebrates, electrical responses to flashes of light on the skin surface have been found in fishes, amphibians, birds and mammals (4,14). Behavioral responses to dermal stimulation by light have been observed in pigeon squabs and new-born rats (10,11) and more recently in the tail of a sea snake, *Aipysurus laevis* (22).

We have been studying thermoregulatory behavior in the small, diurnal Wall lizard, *Podarcis muralis*. Like many lizards, *P. muralis* is heliothermic, utilizing solar radiation either directly (by basking) or indirectly (by positioning itself on warm substrates or warm microclimates) to raise its body temperature to an 'activity temperature range' of 33–38°C (2,18,19). The effectiveness of this behavior is determined largely by the animal's orientation relative to heat source; physiological adjustments such as changes in dermal blood flow or blood shunts are relatively

unimportant (3,9,17). During the course of these investigations it was noticed that the lizards are able to position themselves accurately beneath a tungsten bulb used as a heat source, even when the area of light was so restricted that the head was not exposed. This ability was retained when the radiant heat was removed with filters, suggesting that *P. muralis* used dermal photoreception to position itself relatively to a light source.

To test whether dermal photoreception is used in thermoregulatory behavior, we measured the ability of *P. muralis* to position itself beneath a focal light source when its skin was either occluded or exposed.

MATERIALS AND METHODS

Adult Wall lizards (*P. muralis*) were captured in the surroundings of Florence (Central Italy) and maintained in the laboratory (as described in [18]). Adults animals of this species have a body length from snout to the pelvic girdle of about 60 mm. Lizards ($N = 6$) were introduced singly into an experimental arena measuring 800 × 800 mm. A small pool of light measuring 60 × 20 mm (i.e., about the same dimension of the experimental animals) was projected from a fibre-optic (light source was a Flexilux 600, Scholly, 150 W bulb powered from a 20 V supply) in the center of a patch of warmth (100 × 100 mm) provided

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from an underfloor heater (VIV 10 W, Ultratherm Ltd; without the heater the lizard was not induced to bask). Light intensity at the level of the lizard was about 10 mWcm^{-2} (measurements were made with a FT32-017 thermopile, Hilger-Schwarz). Direct measurement of the infrared radiation at the basking site (with thermopile with light filter and 801 Infratrace telethermometer, Kane-May) and measurement of radiation due to any localized heating of the floor or the dorsal surface of lizard (series 80 pyroelectric vidicon infrared camera, Insight Vision System, Ltd) when the underfloor heater was not switched on showed that the infrared component of the fibre-optic output and heating element were undetectable (the minimum localized heating detectable with this equipment is about 0.3 K [13]).

Light of different spectral composition at the basking site was achieved by filtering the light with wavelength-selective gelatin filters with cut-off points at 480, 540, 600 nm, an infrared filter (cut-off point at 720 nm), and a clear gelatin filter as control. Transmission spectra of the four filters used in the wavelength range 400–700 nm were recorded with a Pye Unicam (SP8-200) spectrophotometer (see [19] for further details and for the transmission spectra). Intensity was maintained at 10 mWcm^{-2} by adjusting the height of the source.

Experimental Protocols

The first 25 occasions during which each lizard entered the patch of light were video-taped. Four days afterwards, we occluded with black acrylic paint (Ivory Black, Windsor & Newton) the entire dorsal surface of the animal (from immediately behind the head to the base of the tail and the lateral surfaces from the pectoral to the pelvic regions). The paint was washed off with water at the end of each day. Transmittance measurements of equivalent layers painted onto glass and onto shed lizard skin showed that there was no transmission of visible wavelengths. We recorded the effects on basking behavior of the following experimental treatments: (i) painting the dorsal surface; (ii) painting different parts of the dorsal surface; (iii) lateral and ventral illumination; (iv) light of different spectral composition; and (v) light of different intensities.

Each animal was tested in 25 trials for each experimental variable. In each trial we recorded: the percentage of the body exposed under the light; the time to expose 25, 50, 75, and 100% of the dorsal surface under the light; and the part of the body exposed under the light (head, middle, rear).

RESULTS

Experiment 1. The Effects of Painting the Dorsal Surface

Painting the dorsal surface reduced the number of basks during which the lizards positioned themselves with the entire body within the pool of light from 83% and 79% in untreated and control (paint on the flanks but not on the dorsal surface) lizards to 46% (Fig. 1A; $N = 150$ for all conditions; χ^2 tests, $P < 0.001$); with no significant differences between individuals (tests of mutual independence, $P > 0.1$ in all cases). It took those dorsally painted lizards which eventually achieved positioning of their entire dorsal surface within the patch of light longer to do so (Fig. 1B; U -test for time to reach 25, 50, 75 and 100% of the dorsal surface in light, $Z = 0.47, 4.61, 6.97,$ and 6.75 respectively, $P < 0.001$ for all except the first case). The head was exposed under the light for the greatest fraction of the time in all three groups; the front and the rear half of the dorsal surface were exposed for proportionately less time in dorsally painted lizards

than in unpainted or control animals (Fig. 1C; χ^2 tests, $P < 0.001$).

Experiment 2. The Effects of Painting Different Parts of the Dorsal Surface

If three-quarters of the dorsal surface was covered with paint, leaving a band 15 mm in length unpainted, the "unpainted band"

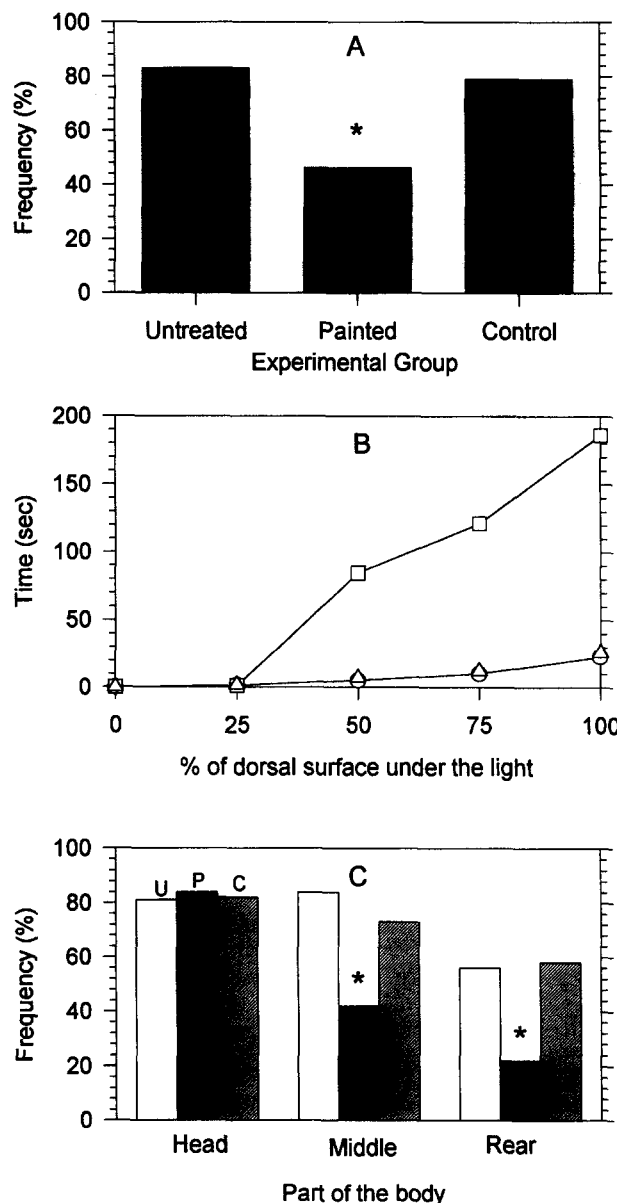


FIG. 1. (A) Percentage of basks in which the entire dorsal surface was eventually positioned under the light in untreated, experimental (paint on the entire dorsal surface), and control (paint on the flanks but not on the dorsal surface) lizards. (B) Mean times (in s) taken to expose 25, 50, 75 and 100% of the dorsal body surface in experimental (□), untreated (○), and control (△) lizards. (C) Percentage of total basking time for which the head, the middle of the dorsal body surface and rear half of the dorsal body surface were exposed in untreated, painted and control lizards. The asterisks denote a significant difference at the level of $P < 0.05$ (see results section for the statistical tests used).

of the dorsal surface was exposed under the light more frequently than the other regions ($\chi^2 = 13.1$ to 34.2 , $P < 0.001$ in all cases). The unpainted bands were exposed more frequently than the painted parts independently by their position on the dorsal surface ($\chi^2 = 14.5$ – 29.3 , $P < 0.001$, in all cases). Unpainted bands were exposed for proportionally more time than adjacent painted segments in all cases ($\chi^2 = 12.5$ to 24.5 , $P < 0.001$ in all cases). When the width of the unpainted strip was reduced to 10, 5 and 3 mm (in random order), only the latter treatment had a significant effect on the frequency with which the unpainted band was exposed ($\chi^2 = 18.5$, $P < 0.001$), and only under this condition was the exposure of the unpainted band not greater than that of adjacent unpainted strip ($\chi^2 = 0.11$, $P > 0.1$).

Experiment 3. The Effect of Lateral or Ventral Illumination

Repeating these experiments using intact lizards with lateral illumination or illumination from below (shining the light through a floor of plastic netting) showed that basking ability was impaired in both cases; frequency of basks resulting in complete exposure was 46% and 6%, respectively ($\chi^2 = 48$ and 165 , $P < 0.001$ in both cases).

Experiment 4. Effects of Light of Different Spectral Composition

Further experiments using light of limited spectrum showed that removing light of wavelengths > 480 nm did not effect the

proportion of basks by intact lizards achieving complete exposure (Fig. 2A; χ^2 tests, $P > 0.1$ in all cases), but removing radiation wavelengths < 720 nm resulted in significant reductions in positioning ability (Fig. 2A; tests for homogeneity with STP analysis, $P < 0.001$).

Experiment 5. Effects of Light of Different Intensities

Reducing the intensity of light containing all wavelengths to 5 mWcm^{-2} had no effect on positioning ability (Fig. 2B; $\chi^2 = 0.76$, $P > 0.1$), but further reduction to 2.5 mWcm^{-2} resulted in a substantial impairment (Fig. 2B; χ^2 for 10 vs. $2.5 \text{ mWcm}^{-2} = 48.8$, $P < 0.001$).

DISCUSSION

These results demonstrate that the dorsal surface of *P. muralis* is capable of responding to bright illumination and mediating the positioning of the body under a fibre-optic light. This capability extends the entire length of the dorsal surface between the pectoral and pelvic girdles. It is impaired by painting the entire dorsal surface of the body with opaque black paint, or allowing only a very narrow band to remain unpainted. The frequency of positioning the head under the light was not affected by painting the body. There are two possible explanations for this (they are not mutually exclusive). One is that dorsal surface of the head is not sensitive to light; the other is that exposure of the head is easily mediated by information from the lateral eyes. Possible sensitivity of the dorsal surface of the tail has not been investigated.

The photo-sensitivity of the dorsal skin is wavelength-dependent. That the skin is responding to the visible spectrum and not to infrared is shown by the fact that the lizard's ability to bask is impaired when wavelengths < 600 nm are removed and unaffected by changes in the infrared. Thus, the ability to expose the body under the light is not mediated by skin heat receptors which detect small changes in the temperature of the skin, but by skin photoreceptors.

The protocol of these experiments does not completely preclude the use of the lateral eyes in mediating the behavioral response; the ability of lizards to position themselves correctly on about 20% of the occasions when the entire dorsal had been painted suggests that there is always some lateral eye involvement. There is also the possibility that the parietal eye is involved. The parietal eye is a photoreceptor (6,15), and its occlusion alters the set point temperatures around which *P. muralis* thermoregulates (19). The results here indicate clearly, however, that information from the lateral and the parietal eyes are not the only sensory modalities involved. We did not perform experiments with blinded lizards for ethical reasons; and because lizards in which the lateral eyes were blindfolded with foam rubber or aluminum foil cups spent most of the subsequent time trying to remove them. Furthermore, observations of lizards blinded by natural infections suggest that they would be totally unresponsive.

The primary biological significance of nonvisual photic responsiveness in lizards must be that it increase the effectiveness of thermoregulatory basking by increasing the precision with which the body can be placed in small patches of sunshine. This would be especially important for relatively elongated lizards such as *P. muralis* living in fairly densely vegetated environments in temperate climates. Efficient basking in such lizards can be crucial for overall Darwinian fitness (12) and should be subjected to intense selection pressure. It also possible that the nonvisual photic sensitivity recorded here might be involved in

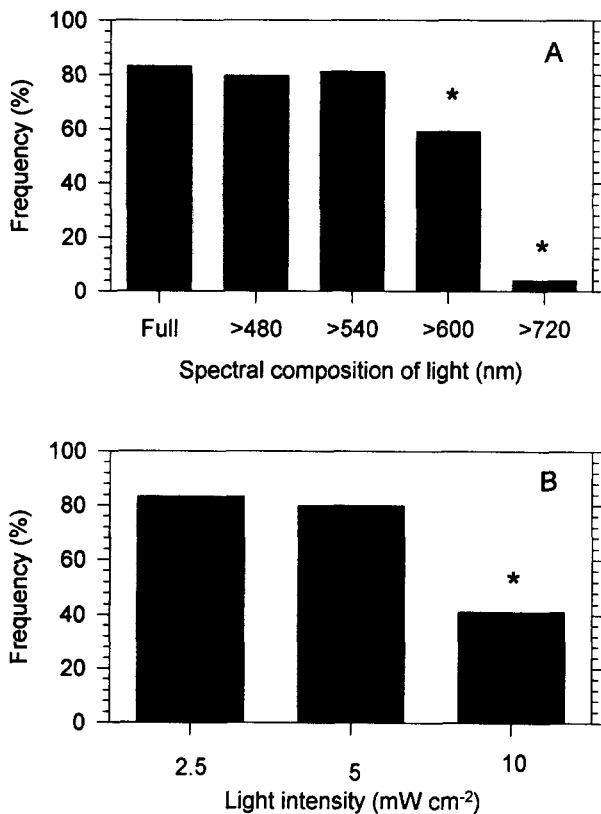


FIG. 2. Percentage of basks in which the entire dorsal surface was eventually positioned under the light in relation to (A) the spectral composition and (B) intensity. The asterisks denote a significant difference at the level of $P < 0.05$ (see results section for the statistical tests used).

the mediation of other functions. For example, extra-retinal photoreceptors entrain circadian activity rhythms in lizards (7,8,20,21). The mechanism of dermal photo-sensitivity recorded here is at present unknown, as is the case for all recorded instances of apparent dermal light sensitivity. Unknown is also the anatomical localization and the electrophysiological properties of these photoreceptors.

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