display chaotic dynamics by the mechanism described here and may displace species like *Agrostis* from productive habitats. Furthermore, both fire and grazing reduce litter mass[17,18], and should decrease the likelihood of chaotic dynamics in native grasslands. Native species that evolved with fire and grazing may be more likely to be inhibited by litter and displaced from habitats after fertilization, fire suppression, or cessation of grazing or mowing. Further work is needed to determine the generality of the patterns we report, to elucidate the role of chaotic dynamics versus stochastic factors in contributing to the fuzziness of patterns observed in nature, and to study the role of litter inhibition in structuring plant communities. □

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Retinal receptors in rodents maximally sensitive to ultraviolet light

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HIGH sensitivity to near-ultraviolet light is a fundamental feature of vision in many invertebrates[1,2]. Among vertebrates there are some amphibians, birds and fishes that are also sensitive to near-ultraviolet wavelengths[3–6]. This sensitivity can be achieved through a class of cone photoreceptor containing an ultraviolet-sensitive pigment[7–9]. Although these receptors were thought not to exist in the eyes of mammals, we now report that some rodents have a retinal mechanism that is maximally sensitive to ultraviolet light.

We measured the spectral sensitivity of pigmented house mice (*Mus musculus*) using a gross electrical potential, the electroretinogram (ERG). The electrical response to a flickering monochromatic test light sensed by an electrode placed against the surface of the eye was compared with that generated by an interleaved, similarly flickering, achromatic reference light[10]. Over successive stimulus presentations the intensity of the test light was varied until the response it produced just matched that produced by the fixed reference light. Repetition of this procedure for many test wavelengths can yield a reliable spectral sensitivity curve that accurately reflects the contributions from the various photoreceptor classes that operate under conditions of light adaptation[11].

Spectral sensitivity functions were obtained from five light-adapted mice (Fig. 1). There are two sensitivity maxima found at about 510 and 370 nm, suggesting that two distinct spectral mechanisms are contributing to the potential under these conditions. If this is the case, then the substantial separation between the two peaks should enable the system responsible for the shorter of the two maxima to be isolated by chromatically adapting the eye. The ERG flicker photometric procedure was used to measure spectral sensitivity for five additional mice whose eyes were exposed to a bright orange adaptation light. Under these conditions sensitivity is sufficiently depressed at long wavelengths that ERG signals cannot be recorded to lights of wavelengths longer than about 440 nm. What remains after such adaptation are spectral sensitivity functions (Fig. 1, lower curve) that are virtually identical for all the mice—they peak at about 360 nm with a very rapid falloff (>0.3 log unit per 10 nm) in sensitivity towards the longer wavelengths.

The results of Fig. 1 indicate that spectral sensitivity in the light-adapted mouse probably results from the combined operation of two mechanisms, one giving peak sensitivity (λ_{max}) at around 511 nm and the other in the ultraviolet. There are other explanations for this result[5]: for example, high ultraviolet sensitivity may represent the secondary absorbance peak (β band) of a photopigment having its principal peak in the visible spectrum; it may come from a photosensitive product which results from bleaching of the long-wavelength pigment, or it may arise because ultraviolet light causes some ocular structure(s) to fluoresce and this fluorescence could be emitted at a longer wavelength at which the pigment absorbing in the visible is sensitive. The relative heights of the two sensitivity peaks (Fig. 1, top) argue against the first explanation and the results of the chromatic adaptation experiment against the third. To test these three possibilities, we measured the sensitivity of the mouse ERG under each of four conditions. Thresholds were determined in two mice for 370- and 510-nm test lights flickering at 12.5 Hz

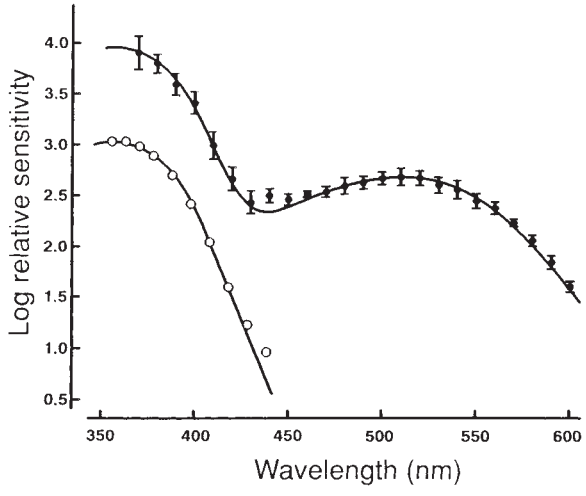

FIG. 1 Spectral sensitivity functions for mice obtained from ERG flicker photometric recordings. Top curve: solid circles are mean sensitivity values for 5 mice; error bars enclose ±2 s.e. The test stimuli were monochromatic lights (half bandwidth 10 nm); the reference light was achromatic (corneal radiance, 0.05 mW). The flicker rate was 25 Hz. Ambient light in the room gave an additional constant luminance of 60 cd per m^2 at the cornea of the test eye. The solid line represents the best least-squares fit to the data of a template constructed by summing two photopigment curves (λ_{max} of 359 nm and 511 nm). These component curves were obtained from photopigment nomograms[19] that had been translated along a log wavenumber axis[20] to the appropriate peak locations. Lower curve: mouse spectral sensitivity function measured while the eye was concurrently adapted to long-wavelength light (produced by a high-pass filter of 50% transmittance at 590 nm; corneal radiance, 6.2 mW). The adapting light (circular, 53°) was spatially coincident with the test and reference lights. Open circles represent mean values for 5 animals; the line is the best-fitting template curve derived as already described. The two sensitivity functions have been arbitrarily positioned on the ordinate.

in the presence of ultraviolet and yellow adaptation lights, the idea being that if there are two mechanisms that can be separately influenced, then sensitivity should alter more when the test and adaptation lights are from the same part of the spectrum than when they are not. That was the outcome: with 510 nm adaptation, the mean threshold change for the 510 nm test light was 1.19 log units, but the same adaptation had essentially no effect (average change of 0.01 log unit) on sensitivity to the 370 nm test light. Ultraviolet adaptation caused average threshold increases of 0.77 log unit (for 370 nm) and 0.37 log unit (for 510 nm). Note that in each case the homochromatic condition gives a greater loss in sensitivity than in the equivalent heterochromatic conditions and that there is no enhancement of sensitivity for heterochromatic adaptation, as would be expected if the bimodal spectral sensitivity function arose simply from a photoproduct. These results indicate that the spectral sensitivity function in the mouse depends on two photopic mechanisms—probably two types of cone—which are maximally sensitive in the near ultraviolet and at about 510 nm, respectively.

To see if the retinal mechanism sensitive to ultraviolet light might have some functional purpose, we tested mice in a behavioural test to see whether they could detect ultraviolet light[12]. Spectral sensitivity functions for two mice are shown in Fig. 2. The functions are qualitatively similar to those from retinal recordings. The mice show two regions of peak sensitivity, one at about 510 nm and the other in the ultraviolet at the shortest wavelength at which it was possible to run the test (370 nm). These results establish that the ultraviolet-sensitive mechanism in the retina detected in electrophysiological measurements can contribute to vision in the mouse.

Is this ultraviolet-sensitive mechanism unique to the mouse? We recorded ERGs from three other rodent species which differ in their visual lifestyles and retinal construction—rat (*Rattus norvegicus*), gopher (*Thomomys bottae*) and gerbil (*Meriones unguiculatus*). These species have a different spectral position for the longer photopic system, but they all seem to show an ultraviolet response spectrally similar to the mouse (Fig. 3), although Fig. 3 indicates that its relative contribution to the ERG varies from species to species, perhaps because the relative proportions of sensitive cones can vary.

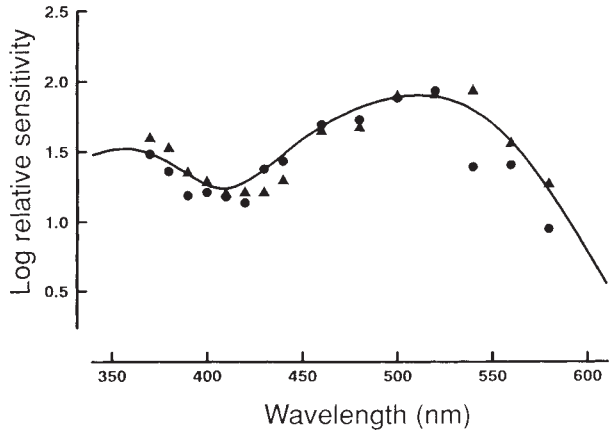

FIG. 2 Spectral sensitivity functions from mice in a behavioural test. Monochromatic stimuli were detected in a forced-choice discrimination task. The mice viewed three stimulus panels which were continuously illuminated with an achromatic light (4,800°; 8.2 cd per m^2). On each trial a monochromatic test light was added to one panel. The animal's task was to indicate which of the panels had been illuminated by touching that panel. The test light was varied in wavelength and intensity over trials. The animal's ability to discriminate each of 15 test wavelengths was established by determining the intensity of the test light required to yield performance significantly better than chance ($P < 0.05$). The symbols are mean thresholds for each of two subjects. The line through the data is the best fit of the template function derived from summing two photopigment sensitivity curves (Fig. 1).

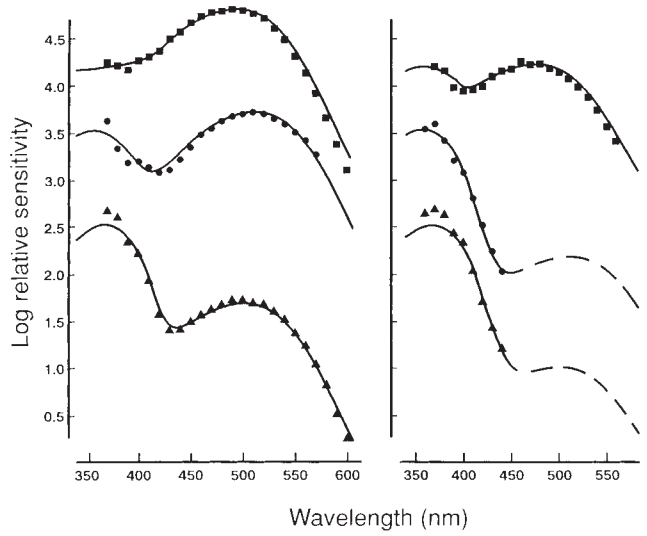

FIG. 3 ERG spectral sensitivity functions obtained from three rodent species (squares, gerbil; circles, rat; triangles, gopher) under test conditions involving achromatic adaptation (left) or long-wavelength adaptation (right). The adaptation conditions are described in Fig. 1. The templates best fit to the data were derived as for Fig. 1, except that for the gerbil the longer of the two nomogram photopigments had λ_{max} of 493 nm; for the gopher this pigment had λ_{max} of 500 nm. Functions are arbitrarily positioned on the ordinate.

Our experiments involve only a small sample of rodents, but an ultraviolet-sensitive mechanism may not be uncommon in the retinae of this group. This mechanism is maximally sensitive to ultraviolet light and enables short-wavelength light to be detected. Although the role(s) of this system in normal vision is unclear, it may explain certain other experimental observations[13–15]. Earlier behavioural and electrophysiological experiments showed that rats[16] and gerbils[17] have only a single photopic mechanism active over the range from 440 to 600 nm, so they were accordingly classified as cone monochromats without colour vision. Our discovery of a second spectral mechanism maximally sensitive in the ultraviolet means that these rodents may have dichromatic colour vision. Other mammals have dichromatic colour vision which is based on signals from a short-wavelength cone (λ_{max} of 420–450 nm) and a cone type absorbing maximally at some longer wavelength[18], so the rodent mechanism of colour vision may be unique among mammals. □

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