with a 500 nm pigment, we demonstrated that dark-adapted humans can see a laboratory hot plate heated to 375 °C. *In situ* measurements of ambient light levels and the spectral characteristics and attenuation at hydrothermal vents are only just beginning[25].

We have demonstrated that the vent shrimp, *Rimicaris exoculata*, previously thought to be eyeless, has a thoracic eye that is well adapted for detection of very dim light. Thermal radiation from high-temperature plumes at black smoker chimneys could provide the light sensed by the shrimp. The role of the thoracic eye as a visual organ, however, will remain unresolved until more is known about its physiology and its unusual photic environment.

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The visibility of 350 °C black-body radiation by the shrimp *Rimicaris exoculata* and man

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The eye of the 'eyeless' shrimp *Rimicaris exoculata* is unusual in having no image-forming optics and a high concentration of rhodopsin[1]. The shrimps swarm around 350 °C hydrothermal 'black smoker' vents in the Mid-Atlantic Ridge[2]. There is no other known source of visible light in the shrimp's environment. The spectral sensitivity of rhodopsin is well matched to typical spectra of bioluminescence of organisms found at lesser depths, but other animals detect such emissions without the unusual features of the *R. exoculata* eye[1]. These two features are most easily understood as an adaptation for the detection of extremely faint sources of light. Physical calculations presented here indicate that the shrimp could see the black-body radiation of the 350 °C vents, even though these sources are practically invisible to the human eye. This would be useful to the shrimp as it feeds on sulphide-loving bacteria very near to the vents[3] but must avoid the lethal 350 °C vents themselves.

In the absence of behavioural evidence, no calculation can prove that the shrimp sees anything. Therefore we take the opposite approach, assuming reasonable values for the few unknown parameters, to show that the known physical constraints do not preclude rhodopsin-mediated detection of 350 °C black-body radiation by *R. exoculata*. We begin with the spectra of black-body emission and rhodopsin photosensitivity, and the amount of rhodopsin (50 pmol) in each shrimp eye[1]. We assume only that the black smoker is a black-body radiator, that there is no intervening absorption over visible wavelengths by the deep sea water or the carapace of the eye, that a reflective layer at the back of the eye (which is apparent in photographs of live shrimp[1]) reflects all light incident upon it, that the dark light (spontaneous isomerizations) in the shrimp eye is comparable to that in other rhodopsin-based eyes, and that the shrimp's nervous system allows it to count (integrate) isomerizations from the entire eye.

A related question is whether this radiation would be visible to man. Partially dark-adapted operators of the Alvin submarine, parked next to the vent, were unable to see anything without artificial illumination (C. L. Van Dover, J. R. Delaney, L. M. Smith, J. R. Cann and D. B. Foster, manuscript in preparation and ref. 4). They did manage, however, to image the hydrothermal vent itself by a long-exposure photograph on a CCD (charge-coupled device) camera.

The spectral photon radiance of blackbody radiation is:

$$N_{e\lambda}(T,\lambda) = 2c\lambda^{-4}(e^{hc/kT\lambda} - 1)^{-1}\ \mathrm{sr}^{-1}, \qquad (1)$$

where T is temperature, λ wavelength, h Planck's constant, c the speed of light, k Boltzmann's constant, and sr is a steradian[5]. The dashed curve in Fig. 1*a* shows this spectrum for a 350 °C black body, relative to its maximum at wavelength 5,889 nm (wavenumber 0.17 μm^{-1}), well outside what is usually considered the visible range. The relative quantum efficiency $\alpha(\lambda)$ of rhodopsin is shown as a dotted curve, peaking at 500 nm (wavenumber 2 μm^{-1})[6]. Absorption is proportional to the product of radiation and quantum efficiency, and is shown as the dotted-and-dashed curve in Fig. 1*a*, relative to its maximum at 588 nm. Note that although the radiation and efficiency curves have very different peaks, at opposite ends of Fig. 1*a*, their tails overlap and have nearly complementary slopes, resulting in a nontrivial absorption peaking at an intermediate wavelength within the 'visible' range. We have not taken into account the transmission of the intervening water or optics—the carapace over the eye—because we do not have good *in situ* measurements over the relevant wavelengths. Distilled water is, however, transparent over the relevant range (200-1,500 nm) and the transmission outside this range has a negligible effect on the calculated total absorption at 350 °C.

Taking into account the radiation and efficiency, the equivalent number of 500 nm photons $s^{-1}\ m^{-2}\ sr^{-1}$ is:

$$N_e(T) = \int_0^\infty \alpha(\lambda) N_{e\lambda}(T,\lambda)\, d\lambda \qquad (2)$$

Assuming the eye is directed toward the 350 °C vent, that the vent is a sphere whose radius subtends an angle ω at the eye, and that the light makes two passes through the rhodopsin (before and after reflection at the back of the eye), the number of photons absorbed is:

$$N_a(T) = 2.9 \times 10^{-6}\ \mathrm{m^2\ sr}\ \sin^2(\omega) N_e(T) \qquad (3)$$

This is plotted in Fig. 1*b* as a function of temperature, assuming that the vent is sufficiently close to fill the shrimp's visual field,

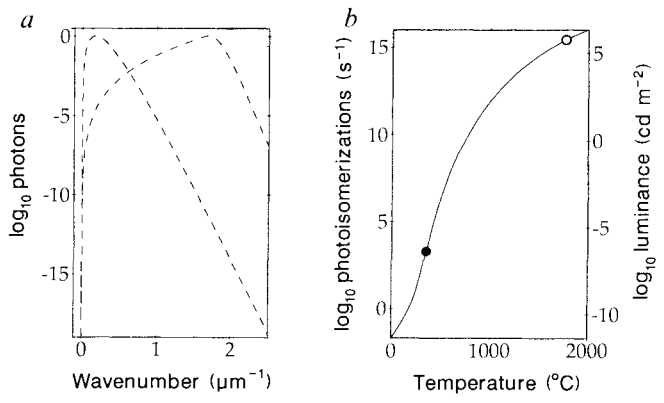

Fig. 1 *a*, The dashed line is the spectral photon radiance $N_{e\lambda}(T, \lambda)$ of 350 °C black-body radiation as a function of wavenumber, $1/\lambda$. The dotted line is the quantum efficiency $\alpha(\lambda)$ of rhodopsin. The dotted-and-dashed line is the product $N_{e\lambda}(T, \lambda)\alpha(\lambda)$. All three plots are relative to their maximum values. *b*, The number of photoisomerizations per second $N_a(T)$ in the shrimp eye (left-hand scale, assuming $\omega = \pi/2$) and the luminance $L'(T)$ (right-hand scale) as a function of the temperature of the black-body radiator. At 350 °C (●) the shrimp eye absorbs 1,800 photons per second under optimal conditions and the luminance is 0.43×10^{-6} cd m^{-2}. The open symbol (○) is explained below.

Methods. Taking into account the angular subtense ω of the target and the area A of the eye, the 500-nm-equivalent photon flux incident on the eye is $N(T) = \pi \sin^2(\omega)$ sr $\times AN_e(T)$. The total number of photons that are absorbed and isomerize rhodopsin in two passes (before and after reflection by the reflective layer) will be $N_a(T) = (1 - t_r^2)\gamma N(T)$, where γ is the quantum efficiency for isomerization and t_r is the transmission of the rhodopsin, which is given by $t_r = 10^{-\varepsilon Cd}$, where ε is the molar absorbance at 500 nm, C is the concentration, and d is the path length. As the transmission is nearly 1, we neglect self-screening and make the approximation $(1 - t_r^2)\gamma = (1 - 10^{-2\varepsilon Cd})\gamma \approx 2\ln(10)\varepsilon Cd\gamma$. The product $\varepsilon\gamma$ is called photosensitivity and is approximately 4.06×10^4 l cm^{-1} mol^{-1} at 500 nm for rhodopsin *in vivo*[9]. Thus $N_a(T) = (2\ln(10)\varepsilon\gamma Cd)N(T)$, which yields equation 3. The area A and thickness d of the rhodopsin layer in the eye cancel out; all that matters is the total amount of rhodopsin. We estimated the efficiency $\alpha(\lambda)$ of the rhodopsin by a Dartnall nomogram peaking at 500 nm, using Dartnall's long-wavelength extrapolation of that nomogram[6], that is, an asymptotic gradient $\Delta\log[\alpha(\lambda)]/\Delta(1/\lambda)$ of 1.05×10^{-3} cm. As a check, note that at 2,042K = 1768.85 °C (the open symbol, ○) the luminance is approximately 60,000 cd m^{-2}, in agreement with the 1967 definition of the candela[5]. The scotopic quantum efficiency of a standard human observer $W'_\lambda(\lambda)$ is approximately equal to the 500-nm rhodopsin quantum efficiency curve $\alpha(\lambda)$, except at short wavelengths (<500 nm), where lens absorption reduces efficiency, and at very long wavelengths (>780 nm) where $W'_\lambda(\lambda)$ is zero[5]. Substituting the standard scotopic relative quantum efficiency function $W'_\lambda(\lambda)$ for $\alpha(\lambda)$ in the definition of $N_{e\lambda}(T, \lambda)$ would have a negligible effect on the computed luminance at temperatures in the range 500 to 2,000 °C, but would have an ever-increasing effect at temperatures below 500 °C. At 350 °C the scotopic luminance is 0.43 10^{-6} cd m^{-2} assuming $\alpha(\lambda)$ but would be only 0.16×10^{-6} cd m^{-2} if we were to assume $W'_\lambda(\lambda)$ instead.

that is $\omega = \pi/2$. At 350 °C the photoisomerization rate is 1,800 s^{-1} (● in Fig. 1*b*).

We assume that isomerizations caused by photon absorption are indistinguishable from thermal isomerizations. Using the Baylor estimate[7] of the rate of thermal isomerization of rhodopsin (in monkey rods), 50 pmol of rhodopsin present in the shrimp eye will yield approximately 1,600 thermal isomerizations per second. To detect the 350 °C vent, the shrimp would have to discriminate a signal-plus-noise isomerization rate of 1,800+ 1,600 = 3,400 s^{-1}from a noise-alone rate of 1,600 s^{-1}. A brief integration time of only 20 ms would yield a decision variable with a signal-to-noise ratio of 6.4 (the mean signal divided by the standard deviation of the noise). This would allow the shrimp to detect correctly the lethal hot water 99.9% of the time, and to mistake ambient for hot water only 2% of the time. The photon flux and signal-to-noise ratio will, however, fall quickly if the shrimp is farther from the vent. Assuming a long integration time of 1 s, then for the shrimp to obtain a minimum useful signal-to-noise ratio of 1 (correctly detect hot water 50% of the time and mistake ambient for hot 16% of the time) the 350 °C vent must subtend at least $2\omega = 2.5°$. Thus a 10 cm wide vent could be detected from as far away as 2.3 m.

To assess the visibility of the vent by man we estimate its scotopic luminance:

$$L'(T) = \frac{1{,}700\ \text{lm}}{\text{W}} \frac{hc}{507\ \text{nm}\ \alpha(507\ \text{nm})} \frac{N_e(T)}{} \qquad (4)$$

where lm is a lumen. This is plotted in Fig. 1*b* over the temperature range 0 to 2,000 °C, using the right-hand vertical scale. At 350 °C (●) the luminance is 0.43×10^{-6} cd m^{-2}, which is slightly below the average threshold of 0.75×10^{-6} cd m^{-2} found by Pirenne[8] for seeing a large long-duration uniform disk by fully dark-adapted observers with natural pupils and unrestricted eye movements. Thus the operators of the Alvin submarine failed to see the vents by naked eye[4] because the vents were just below the threshold of visibility.

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Segment-specific expression of a zinc-finger gene in the developing nervous system of the mouse

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The process of segmentation, in which repeated homologous structures are generated along the anterior–posterior axis of the embryo is a widespread mechanism in animal development. In vertebrates, segmentation is most apparent in the somites and the peripheral nervous system[1,2], but the existence of repetitive bulges, termed neuromeres, in the early neural epithelium of vertebrates suggests that the CNS may also be segmented[3–9]. Consistent with this, cranial ganglia[8] and certain neurons[8,10] are associated with specific hindbrain neuromeres. Here, we report that *Krox*-20, a zinc-finger gene, is expressed in two alternate neuromeres in the mouse early hindbrain. This pattern subsequently decays and *Krox*-20 is transiently expressed in specific hindbrain nuclei. In addition, *Krox*-20 is expressed in early neural crest cells, and then in the neural crest-derived boundary caps, glial components of the cranial and spinal ganglia. The demonstration that neuromeres are domains of gene expression provides molecular evidence for the segmentation of the CNS.