

**Figure 2** Short-period P-wave seismograms from K980822. Recording stations: **a, b**, HFS,  $D=36.8^\circ$ ,  $A=311.3^\circ$ ; **c, d**, ILAR,  $D=60.7^\circ$ ,  $A=20.2^\circ$ ; and **e, f**, ASAR,  $D=88.4^\circ$ ,  $A=130.4^\circ$ .  $D$  is the epicentral distance and  $j$  is the source to station azimuth. **a, c, e**, Seismograms have been processed using an optimum filter<sup>3</sup> to attenuate low-frequency noise. An additional lowpass filter cutting off at 3 Hz has been applied to the ASAR seismogram. **b, d, f**, Product of the semi-sums. Amplitude ranges were used to test for compatible double-couple sources. HFS P, 1.5–3.0; pP, 0.0–2.0; sP, 0.0–2.0. ILAR, P, 3.0–4.0; pP, 0.0–1.0; sP, 0.0–1.0. ASAR, P, 1.0–2.5; pP, 0.0–1.5; sP, 0.0–1.5. All amplitudes are in arbitrary units. Polarities are assumed to be unknown except for P at ILAR, which is taken to be positive.

This indicates that the source is so shallow that surface reflections arrive within 1.7 s of the onset, which should arouse suspicion.

The analysis shows that explosions with yields well below 1 kilotonne can be recognized as suspicious. In contrast, the Non-Proliferation Experiment<sup>6</sup>, in which 1 kilotonne of conventional explosive fired at the Nevada Test Site in the United States on 22 September 1993, was less well recorded at long range. Its  $m_b$  was 4.1, compared with the 4.6 predicted for an explosion at Degegen Mountain with the same yield.

These results possibly overstate the ability of seismologists to identify small explosions. Knowing when and where the explosion took place means that the signals can be interpreted with more confidence than would be possible when analysing signs of a possible disturbance for which the only information is the seismograms. But

when the IMS and the International Data Centre are fully operational, such disturbances will be recorded by more stations, with wider azimuthal coverage, increasing the confidence of the interpretation.

Anyone attempting a clandestine test could be sure of getting away with it only by using yields well below that used here or by attempting to muffle, or decouple, the test by firing the explosion in a large cavity. A decoupled test using conventional explosives is planned for the site next year. We await the results with interest.

**A. Douglas, D. Bowers, P. D. Marshall, J. B. Young, D. Porter & N. J. Wallis**

*AWE Blacknest, Brimpton, Reading RG7 4RS, UK  
e-mail: alan@blacknest.gov.uk*

1. Douglas, A., Hudson, J. A., Marshall, P. D. & Young, J. B. *Geophys. J. R. Astron. Soc.* **36**, 227–233 (1974).
2. Douglas, A., Marshall, P. D., Young, J. B. & Hudson, J. A. *Nature* **248**, 743–745 (1974).
3. Douglas, A. *Bull. Seismol. Soc. Am.* **87**, 770–777 (1997).
4. Pearce, R. G. & Rogers, R. M. *J. Geophys. Res.* **94**, 775–786 (1989).
5. Pearce, R. G. in *Monitoring a Comprehensive Test Ban Treaty* (eds Husebye, E. S. & Dainty, A. M.) 805–832 (Kluwer, Dordrecht, 1996).
6. Denny, M. (ed.) *Proceedings of the symposium on the Non-Proliferation Experiment (NPE): Results and Implications for Test Ban Treaties* (Lawrence Livermore National Laboratory, US Department of Energy, 1994).

## Seeing movement in the dark

Our visual world is greatly reduced at night. Spatial and temporal resolution are poor, contrast sensitivity is diminished, and colour vision is totally absent<sup>1</sup>, as rod photoreceptors are used rather than the cone photoreceptors that operate during the day. Many aspects of rod vision, including spectral, contrast and flicker sensitivity, have been studied in detail<sup>1</sup>, but motion perception has been largely ignored<sup>2</sup>. We find that motion perception using rods is impaired, with moving objects appearing to be slower than they are during cone vision.

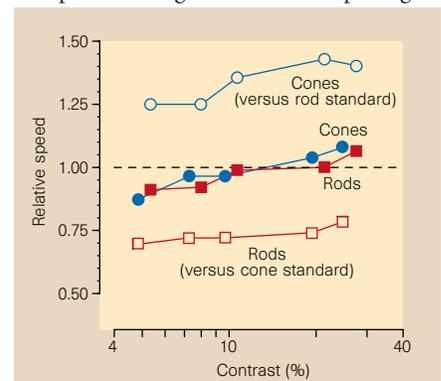
Rod monochromats, who lack cone vision and are totally colour-blind<sup>3,4</sup>, often report problems when dealing with moving objects. To find out whether such problems are encountered by normal observers when restricted to rod vision, we compared the speed of moving objects as seen through rods and through cones.

We used a standard cathode-ray-tube monitor and conditions chosen to isolate either rods or cones. These monitors have only three independent parameters, one each for the red, green and blue phosphors, whereas the human visual system has four: one for the rods and one each for the red, green and blue cones. A direct comparison is therefore impossible in observers with normal colour vision because we cannot stimu-

late the rods in isolation while silencing all three cone classes. We overcame this difficulty by using observers with red–green colour-blindness (dichromats, about 2% of the male population). Our observers were deuteranopes, who lack functional green cones<sup>5</sup>. For such observers, who have normal motion perception for luminance-defined stimuli<sup>6</sup>, it is possible selectively to excite rods while silencing activity in red and blue cones, and to excite red cones while silencing the rods and blue cones.

We used standard psychophysical methods to determine the physical speed at which stimuli selectively activating rod and cone photoreceptors appear to move equally fast. Rod-detected motion stimuli appear to move at about 75% of the speed of a reference motion stimulus detected only by red cones, and red-cone-detected motion stimuli appear to move at about 130% of the speed of a rod-detected reference motion stimulus (Fig. 1). This is also the case at several dimmer light levels, for which the relative visibilities of the rod and cone stimuli vary considerably. There is a subtle but significant dependence on contrast<sup>7,8</sup>, with stimuli of higher contrast appearing to move faster, regardless of whether they are detected by rods or cones.

What causes the poorer performance of the night-vision rod system? A cortical explanation, in which rod- and cone-detected motion are analysed by different systems, is unlikely because the overall dependence on contrast was identical for rods and cones<sup>8</sup>. More compelling is a retinal explanation, in which the slowing may be caused by the spatial and temporal averaging in the distal rod visual system<sup>1,9</sup>. Such low-pass filtering of the visual input signal



**Figure 1** Relative movement of rod and cone stimuli. Perceived speed is shown as a function of percentage rod or red-cone contrast. Reference and comparison stimuli activated either the same (filled symbols) or a different (open symbols) class of photoreceptor (rods or red cones). Space-time-averaged luminance was 0.92 log cd m<sup>-2</sup>, a level at which both rods and cones are active. On each trial, observers judged which of two moving sine-wave gratings (1 c deg<sup>-1</sup>) moved faster. Gratings were presented simultaneously for 1 s and moved in opposite directions. For more details, see ref. 8.

will affect the output of motion detectors driven by rod signals. As a result, the relative signal at slow velocities will be higher than at fast velocities for rod vision, so the stimuli will appear slower.

The use of artificial lighting can help to avoid the disadvantages of rod-mediated vision. Indeed, most tasks can now be performed as well by night as they can by day. But driving at night may be an important exception. The region illuminated by the car headlights is processed mainly by the cones, whereas on a poorly lit road the remaining visual field is in the dark and is processed mainly by rods. The region in the dark includes the sides of the visual fields, where translatory motion signals are largest. This might lead to an underestimation of the speed of movement, which in turn might elicit a compensatory — and possibly fatal — increase in speed<sup>10</sup>.

Karl R. Gegenfurtner\*, Helmut Mayser†, Lindsay T. Sharpe†

\*Max-Planck-Institut für biologische Kybernetik, Spemannstrasse 38, 72076 Tübingen, Germany e-mail: karl@kyb.tuebingen.mpg.de

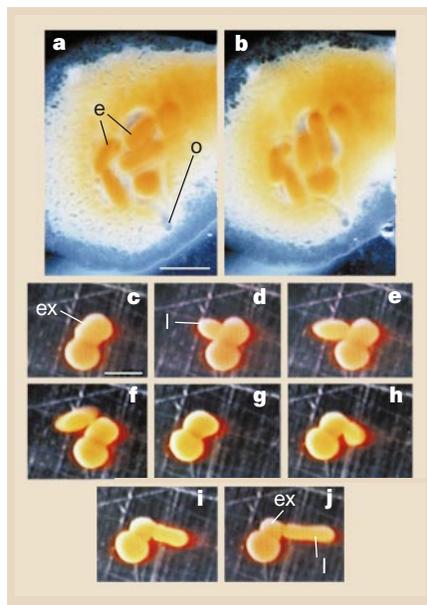
†Universitätsaugenklinik, FEO, Röntgenweg 11, 72076 Tübingen, Germany

- Hess, R. F., Sharpe, L. T. & Nordby, K. *Night Vision: Basic, Clinical and Applied Aspects* (Cambridge Univ. Press, 1990).
- Takeuchi, T. & De Valois, K. K. *Vision Res.* **37**, 745–755 (1998).
- Sharpe, L. T. & Nordby, K. in *Night Vision: Basic, Clinical and Applied Aspects* (eds Hess, R. F., Sharpe, L. T. & Nordby, K.), 335–389 (Cambridge Univ. Press, 1990).
- Kohl, S. *et al. Nature Genet.* **19**, 257–259 (1998).
- Sharpe, L. T., Stockman, A., Jägle, H. & Nathans, J. in *Colour Vision: From Genes to Perception* (eds Gegenfurtner, K. R. & Sharpe, L. T.) 3–48 (Cambridge Univ. Press, 1999).
- Cavanagh, P. & Anstis, S. *Vision Res.* **31**, 2109–2148 (1991).
- Thompson, P. *Vision Res.* **22**, 377–380 (1982).
- Hawken, M. J., Gegenfurtner, K. R. & Tang, C. *Nature* **367**, 268–270 (1994).
- Barlow, H. B. *J. Physiol.* **141**, 337–350 (1958).
- Snowden, R. J., Stimpson, N. & Ruddle, R. A. *Nature* **392**, 450 (1998).

## Sexual propagation by sponge fragments

Habitat fragmentation means that many species occur in discrete populations<sup>1</sup>, so it is important for sessile species to colonize new areas. It has not been clear how sponges whose larvae disperse over short distances achieve this. Fragments may break off sponges as a result of physical and biological disturbance and are then dispersed by currents and recruited as independent individuals or colonies<sup>2,3</sup>. Local populations are expected to have high genetic relatedness as a result, but most sponge populations have high levels of genetic variability<sup>4,5</sup>. We suggest that this discrepancy results from an interaction between fragmentation and sexual reproduction.

We studied reproduction in *Scopalina lophyropoda*, a sublittoral demosponge with



**Figure 1** Time-lapse observations of embryogenesis and larval release. **a, b**, A small sponge reorganized from an explant. Six embryos (e) are incubated in a chamber connected to the exterior through an oscular tube (o). Note the differences in size and repositioning of embryos in the 90 min between pictures. **c–j**, Time-lapse observations over 93 min of two embryos escaping as free-swimming larvae from an unattached explant (ex), which is in contact with another non-histocompatible fragment. Scale bars, 1 mm.

populations sparsely scattered over the western Mediterranean<sup>6</sup>. In this species, embryos are incubated and lecithotrophic parenchymella larvae are released from mid-July to late August. Because the planktonic phase lasts only 2.5 days, most larvae are believed to recruit locally. However, the dispersal potential of these larvae is significantly increased by the fragmentation of brooding adults as a result of wave action and foraging by fish and echinoderms.

Tissue shredded artificially reorganizes into dense balls, in which internal epithelia and choanocyte chambers dissociate and most specialized cells regress to an amoeboid, archaeocyte-like morphology. If detached fragments lie immobile on the substratum for a few days, they reattach and reorganize as functional sponges. When fragmentation occurs in reproductive sponges, fragments as small as 1 to 2 mm across may contain several developing embryos. Because development requires nourishment from specialized nurse cells through a placental-like membrane<sup>7</sup>, we expected that the embryos would be reabsorbed and their energy reallocated to reorganize the colony. Instead, embryos were nourished by cells in the tissue fragment, where they completed development to free-swimming larva.

We used forceps to disintegrate sponges in early and late embryogenesis (one month before and 10 days after the onset of larval

release), and randomly selected explants (balls of tissue) 1–2 mm across ( $n = 80$  per group). We found that 52.5% of the explants obtained in early embryogenesis remained embryogenically active and released a total of 102 free-swimming larvae (between 0 and 7 per explant) over a 28-day period. The first two larvae were released on days 4 and 8, before the explants reorganized as sponges. The remaining embryos were incubated for 14–28 days in a translucent, atrium-like chamber formed once explants had reorganized into sponges (Fig. 1a). Nearly mature larvae moved around inside the chamber for several days before being released through an oscular tube (Fig. 1a,b). The atrium then lost its structure and the oscules regressed to being perforations.

When mother sponges in late embryogenesis were shredded to obtain explants, most mature embryos escaped as free-swimming larvae. Only 6.25% of explants contained developing embryos, and just seven larvae were released over a 28-day period, escaping from unattached explants in all cases by crawling through the disorganized mass of cells in the explant (Fig. 1c–j).

Explant attachment took between 3 and 24 days in calm water, with just 2.5% remaining unattached after 28 days, and these were apparently still viable. There were no significant differences in time to attachment between explants that carried embryos and those that did not. It is difficult to estimate possible dispersal distances before attachment, but large sponge fragments can disperse rapidly over several kilometres during heavy storms<sup>3</sup>.

Our results show that even small fragments often carry the essential functional elements for reorganizing and nourishing embryos. Our findings also indicate that fragmentation may interact with sexual reproduction. This means that the dispersal capacity of sexually produced propagules is maximized by the additional dispersal of the asexual propagule. The dispersal of embryo-bearing fragments also maximizes the chance that several distinct genotypes will reach a new area, increasing the chance of establishing new populations.

Manuel Maldonado, María J. Uriz

Centro de Estudios Avanzados de Blanes (CSIC), Department of Aquatic Ecology, Camino de Santa Bárbara s/n, Blanes 17300, Girona, Spain e-mail: maldonado@ceab.csic.es

- Hanski, I. *Nature* **396**, 41–49 (1998).
- Battershill, C. N. & Bergquist, P. R. in *New Perspectives in Sponge Biology* (ed. Rützler, K.) 397–403 (Smithsonian Institution Press, Washington DC, 1990).
- Wulff, J. L. *Coral Reefs* **14**, 55–61 (1995).
- Solé-Cava, A. M. & Thorpe, J. P. *Mar. Biol.* **93**, 247–253 (1986).
- Benzie, J. A. H., Sandusky, C. & Wilkinson, C. R. *Mar. Biol.* **119**, 335–345 (1994).
- Uriz, M. J., Maldonado, M., Turon, X. & Martí, R. *Mar. Ecol. Prog. Ser.* **167**, 137–148 (1998).
- Fell, P. E. in *Reproductive Biology of Invertebrates* Vol. IV, *Oogenesis, Oviposition, and Oosorption* (eds Adiyodi, K. G. & Adiyodi, R. G.) 1–41 (Wiley, New York, 1989).