atic differences in their visual-field representations. In this way, Engel *et al.*³ initially identified V1 and V2, and then determined the colour tuning of these two regions. They used flickering pinwheel stimuli of different contrast (Fig. 1), and measured the fMRI response averaged over the whole of V1 and V2 separately. They found that there was a systematic increase in the fMRI signal with increasing contrast in the stimulus. By repeating this for several different colour combinations, they worked out response contours of equal activity for these brain regions. The result was a map of the activity of two independently identified cortical areas — V1 and V2 — to any colour combination.

What singles out this study is that the fMRI data can be readily correlated with psychophysically obtained measurements. Indeed, the similarity between the psychophysical threshold measurements and the fMRI responses of the same observers to the same stimuli is quite stunning. In both experiments the best responses are obtained for coloured stimuli, the perception of which is mediated by colour-opponent processing. There are also remarkable differences. Most notably, whereas the fMRI data show a bigger response to colour than luminance throughout, psychophysically this holds only for a highly restricted range of stimuli, those with little spatial or temporal variation⁹. Although the fMRI measurements are about 100 times less sensitive than the psychophysical measurements, if we assume that the contours can be directly related to one another, the implication is that there is substantial temporal filtering of the chromatic signal after the V1 region.

The fMRI response to coloured stimuli is also greater than would be expected based on single-cell recordings in Old World monkeys, whose cones and pathways for early visual processing are similar to those in humans. Here, fewer than 15 per cent of all cells give a larger response to colour than to luminance². So why is the fMRI response dominated by the activity of colour-opponent cells instead of luminance cells? To answer this, we need to look at the relationship between single-unit activity and fMRI response. Does the fMRI signal simply reflect the average activity of all neurons? And how specific is the response of an individual neuron to a particular stimulus?

Many of the 'luminance' cells in the V1 region have highly complex receptive-field properties. Their responses are determined by many conjoined properties of the stimulus, including orientation, spatial frequency, temporal frequency, direction and size¹⁰. In single-unit recordings, the idea is to get all of these parameters right for the individual cell, so there will be a strong response to the optimal stimulus but little response to everything else. Because each cell gets its

optimal stimulus, a number of highly active cells are observed. However, it is not clear how many of these cells respond to a particular stimulus, such as the pinwheel used by Engel and colleagues. There might even be an advantage in having a few neurons as possible respond to each luminance stimulus⁶. But the goal could be quite different for colour. Here, the visual system might want to attach a colour to each stimulus, independently of its other characteristics. So it would make sense for colour cells to respond in a less specific manner to these other features.

Although other interpretations of some aspects of these data are possible, the exciting prospect is that we can now study the functional transformation of the response across different visual areas, and correlate the

signals to single-cell responses in these areas as well as to psychophysical responses. □

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Astrophysics

Not-so-cosmic rays

Peter L. Biermann

Cosmic rays are energetic particles that constantly hit the Earth. They include protons and heavier nuclei, along with a few electrons and positrons. It is usually assumed that the flux of cosmic rays is roughly the same throughout our Galaxy, but new data published by Anatolya Erlykin and Arnold Wolfendale may mean that what we see contains the signature of a nearby source, probably a young supernova remnant¹.

Cosmic rays have been seen up to an energy of nearly 10^{21} electron volts (eV) — far beyond any dream of the physicists at the particle accelerators at Stanford, Fermilab or CERN. The flux is very low, from about 10 particles $\text{cm}^{-2} \text{s}^{-1}$ at energies near 10^9 eV, to about 1 particle km^{-2} per century near 10^{20} eV.

More than sixty years ago, Walter Baade and Fritz Zwicky pointed out² that the beautiful nebulae left behind by exploding stars — such as the supernova of AD 1054 observed by Chinese astronomers — could be the powerhouses that accelerate cosmic rays. The standard theory, originally conceived in its basic form by Enrico Fermi about fifty years ago^{3,4}, holds that cosmic rays gain their energy in shock waves created by the explosion of stars. Charged energetic particles gyrate around magnetic fields on both sides of a shock, and bounce off irregularities in the gas. Some of these particles bounce back and forth across the shock, gaining energy all the time because the two flows are moving towards each other — compression heats, as a bicycle pump demonstrates.

Three things limit the maximum energy that a particle can gain in this process. First, it can run out of time: the shock gets slower as it

engulfs more material, and therefore less efficient at accelerating particles. Second, it can run out of room: a charged particle gyrating in a magnetic field needs some space for its helical motion, and this space increases with energy (and decreases with the charge on the nucleus), so at a certain energy the gyration can become bigger than the shock wave. Third, it can hit something

Figure 1 Three knees. The spectrum of cosmic rays hitting the Earth steepens at an energy of about 10^{15} eV (at the 'knee'), and it is relatively easy to explain their production up to about this energy. That could mean: a, that there are two different types of source, which have spectra that join at the knee; or b, that the lower-energy cosmic rays somehow get accelerated, inefficiently, to energies above the knee. But now there is also evidence for bumps, or 'teeth', below the knee, which could be due to different elements accelerated in a nearby supernova remnant. That would mean some changes to either a or b, such as for instance shown in c.

and so lose energy: interactions with ordinary matter and light can brake the acceleration at a maximum energy below the limits imposed by time or space.

Shock acceleration at supernova remnants can explain cosmic-ray energies up to about 10^{15} eV, where, interestingly, the cosmic-ray spectrum suddenly turns downwards (Fig. 1). But we still observe some cosmic rays to energies six orders of magnitude above this 'knee'. Perhaps the higher-energy cosmic rays come from an entirely different source, so the spectrum we see is the sum of two separate spectra (such as the two bottom curves in Fig. 1). Alternatively, acceleration of lower-energy cosmic rays may continue to higher energies, either at shock waves in magnetic stellar winds, or by continuous acceleration in the interstellar medium (by random scatterings from moving magnetic irregularities). In Fig. 1, the central green curve depicts this possibility.

Now the picture may have become more complicated. Erlykin and Wolfendale¹ point out that much of the cosmic-ray flux at Earth could be from the most recent nearby supernova. For cosmic rays coming from a single source, the time and space scales are fixed, so each type of nucleus should have a sharply defined maximum energy, proportional to its charge. This would produce a sawtooth pattern in the spectrum near the knee, each 'tooth' corresponding to an abundant element (Fig. 1, top).

Cosmic rays at these high energies are detected from the 'air showers' that they produce. A cosmic-ray particle enters the Earth's atmosphere and collides with the nucleus of an atom to produce a large number of secondary particles, which hit other nuclei, and so on. At ground level, this translates to a shower of electrons, positrons, photons and muons, whose size depends on the energy of the original cosmic ray. Collating all available data from air-shower experiments, Erlykin and Wolfendale argue that they have discovered 'teeth' corresponding to oxygen and iron near the knee, signs of a recent nearby supernova. Such a supernova would need to be much younger than 10^5 years, and would have to have occurred much closer than 1 kpc. Thus, Vela is a possibility, for instance. If confirmed, this would be powerful evidence for the supernova-remnant theory of cosmic-ray acceleration.

Experimental data now in the pipeline should shed more light on the chemical composition, and thus the origin, of particles with energies from the knee, near 10^{15} eV, up to 10^{18} eV, forming a vital bridge to the highest-energy scales. At the highest energies, above 10^{18} eV, cosmic-ray particles can no longer be contained by our Galaxy's magnetic fields; so as Giuseppe Cocconi realized forty years ago⁵, these particles must come from beyond our Milky Way. It is the goal of the international Auger project — a pair of

detector arrays each covering 3,000 square kilometres, still in the planning stage — to detect these highest-energy cosmic-ray particles. To understand their origin and propagation through the Universe would turn cosmic-ray physics into a tool of fundamental physics at extreme energies. □

Palaeoclimatology

Back at the last interglacial

Joël Guiot

It has been established that, over the past 20,000 years or so, alterations in regional vegetation are controlled by the broad, global pattern of climate change. But what about periods longer than this? Are non-climatic factors such as migration and competition between species involved? The answer to this question is of interest because it can tell us how much we can learn about past climate from the vegetation of the time.

On page 57 of this issue¹, Whitlock and Bartlein describe their analysis of a 125,000-year pollen record of vegetation from Carp Lake in the Pacific northwest of North America. Their conclusion is that climate variations are the cause of the millennial-scale changes in vegetation that they see; that is, the fluctuations between steppe and forest vegetation

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cover, and between subalpine forest and forest types adapted to warm and dry conditions, are strongly correlated with global climate — see Fig. 2 of the paper, page 58. So low ice volume with maximum summer insolation favoured 'warm-and-dry' forest, and moderate ice volume with minimum summer insolation supported subalpine conifers.

It is then possible to assign vegetation to particular climatic events. So-called stage 5e (the Eemian, the last interglacial before the present one, which ran from about 125,000 to 115,000 years ago) was characterized by warm-and-dry, full forest. Stage 5a (the last temperate period before the ensuing full glacial, 85,000–75,000 years ago) was, by contrast, characterized by a warm-and-dry but less dense forest, composed of both trees

Figure 1 Succession of vegetation biomes in La Grande Pile, a pollen sequence from eastern France¹¹, represented along a timescale (x-axis), and the first principal component of pollen taxa (PBO) describing the main fluctuations (from forest to steppe/ tundra) in the pollen data. The biome succession was determined using the method of Prentice *et al.*¹³. The lower panel also shows ice volume over the same timescale, as represented by the same SPECMAP sequence used by Whitlock and Bartlein¹ (see Fig. 2, page 58).