living avian descendants. And, more importantly, locomotion and limb function have evolved like any other features[10].

Most of the fossil footprint literature documents new tracksites, describes the form and proportions of tracks, and tries to assign such tracks to trackmakers, usually with little in the way of direct anatomical reference[2]. At a landmark conference[11] in 1985, there was consensus that two frontiers should receive renewed attention: kinematic patterns and 'competency' of the sediment. Unfortunately, few studies have since done so. But Gatesy *et al.*[5] set the standard for future work, and show just how much we have to gain from such analyses. ☐

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1. Batory, D. & Sarjeant, W. A. S. *J. Arthur Conan Doyle Soc.* **8,** 89–101 (1998).
2. Lockley, M. G. *Tracking Dinosaurs: A New Look at an Ancient World* (Cambridge Univ. Press, 1991).
3. Thulborn, T. *Dinosaur Tracks* (Chapman & Hall, London, 1990).
4. Murie, O. J. *A Field Guide to Animal Tracks* (Houghton Mifflin, Boston, 1968).
5. Gatesy, S. M., Middleton, K. M., Jenkins, F. A. Jr & Shubin, N. H. *Nature* **399,** 141–144 (1999).
6. Jenkins, F. A. Jr *et al. Meddr. Grønland, Geoscience* **32,** 1–25 (1994).
7. Baird, D. T. *Bull. Mus. Comp. Zool.* **117,** 449–520 (1957).
8. Padian, K. & Chiappe, L. M. *Biol. Rev.* **73,** 1–42 (1998).
9. Lockley, M. G., Yang, S. Y., Matsukawa, M., Fleming, F. & Lim, S. K. *Phil. Trans. R. Soc. Lond.* **336,** 113–134 (1992).
10. Padian, K. & Olsen, P. E. in *Dinosaur Tracks and Traces* (eds Gillette, D. D. & Lockley, M. G.) 231–241 (Cambridge Univ. Press, 1989).
11. Gillette, D. D. & Lockley, M. G. (eds) *Dinosaur Tracks and Traces* (Cambridge Univ. Press, 1989).
12. Ostrom, J. H. *Annu. Rev. Earth Planet. Sci.* **3,** 55–75 (1975).

Earth science

Radon and rock deformation

Evelyn Roeloffs

What happens when stress is applied to rocks in the Earth's crust so that the crust deforms? This is a question tackled by Trique *et al.* on page 137 of this issue[1]. They have used a natural laboratory in the French Alps — the Roselend reservoir — to monitor the geophysical signals that result from the greater or lesser pressure on the underlying crust exerted by the weight of water in the reservoir. This area is not itself prone to earthquakes. But the broader interest of this work is in what it may tell us about the events, induced by crustal deformation, that precede earthquakes.

The ability to predict earthquakes is of course highly desirable. But progress in this difficult and highly contentious science will depend on detecting and interpreting physical changes stemming from the processes of earthquake generation. Many possible precursors have been reported, but seismologists are sceptical of those that are not clearly linked to crustal deformation. This 'unproven' category includes the well-documented precursory decrease and increase of radon concentration before the 1978 Izu–Oshima earthquake in Japan[2] (Fig. 1), as well as the controversial assertion that moderate earthquakes in Greece have been predicted from variations in the local electric field[3].

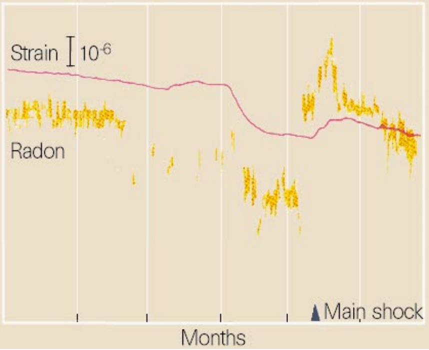

Figure 1 **The radon and strain data for the magnitude-7 Izu–Oshima earthquake[2,9] of 14 January 1978 show changes preceding the earthquake. But they do not match the model shown in Fig. 2; in particular, neither change is monotonic, and in both cases the pre-earthquake change exceeds that produced by the earthquake itself.**

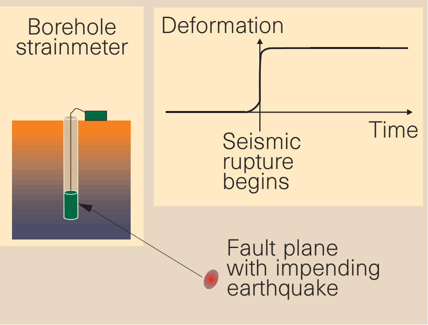

Figure 2 **Rock friction, which depends on slip rate and sliding-induced changes on a fault surface, implies that seismic slip should be preceded by accelerating aseismic slip near the hypocentre of an impending earthquake. Sufficient aseismic slip would produce near-surface deformation detectable by a borehole strainmeter. Compared with the strain step recorded at the time of the earthquake, the precursory strain signal would be in the same direction but of much smaller amplitude. A magnitude-5 earthquake, 10 km deep, produces maximum near-surface strain of about 10^{-7} at a site 5 km from its fault plane; strain increases 30-fold for each unit increase of magnitude, but falls off as the third power of distance from the source. Estimates of pre-seismic slip duration and amplitude range widely because frictional parameters of natural faults are poorly known.**

Trique *et al.*[1] now report that various phenomena — bursts of radon gas, changes of electric potential, and departures of ground tilt from that predicted on an assumption of linear rock elasticity — consistently accompany water-level variations behind the Roselend dam. These phenomena occur together, usually within days after an abrupt change in the reservoir's filling or emptying rate. At Roselend, radon emissions and electrical changes are produced by a well-quantified driving force — the lake 'load', or weight of water — instead of the poorly understood processes that precede earthquakes. But the observations do provide indications of the relationship between radon and electrical anomalies, and the deformation of crustal rocks.

Seismologists expect earthquake precursors to take the form of transient crustal-strain signals from 'aseismic' fault slip near the earthquake's nucleation point (that is, fault slip that is too slow to radiate seismic waves) (Fig. 2). Numerical simulations show, however, that such signals would be exceedingly small[4]. Even the best existing instruments — borehole strainmeters with resolution exceeding a part per billion — would need to be within a few kilometres of the impending earthquake's epicentre to detect this aseismic strain. Although strain changes preceding two California earthquakes have been identified[5,6], they don't resemble the expected signals.

Proponents of earthquake prediction maintain that changes in radon emission, or in electrical or magnetic fields, represent a natural amplification of pre-earthquake deformation under special geological conditions. For example, the conductance by rock fractures of water or gas is proportional to the third power of the fracture's aperture[7]. Fluid flow past ions adsorbed on rock surfaces produces an electric field, termed a 'streaming potential', that varies with pressure gradient and permeability[8]. Fluid, gas or electromagnetic measurements might thus detect deformation indirectly, albeit at localized sites and with amplitudes related nonlinearly to strain.

Silver and Wakita[9] list many potential examples of such pre-earthquake 'strain indicators'. Unfortunately, these indicators are irreproducible: they can be detected only in certain locations, but in any one location earthquakes recur infrequently. What is needed is evidence that transient strain leads consistently, if not linearly or uniformly, to observable phenomena. The radon, electrical and ground-tilt measurements from Roselend lake constitute this kind of reproducible evidence.

The shallow crust's reaction to large changes in lake level may also illuminate the physics of earthquake generation. Although Roselend lake is free of earthquakes, the apparent stimulation of geophysical anomalies by changes in its filling or emptying rate is reminiscent of peculiar seismic features evident at other large reservoirs. Earthquakes larger than magnitude five at Koyna reservoir (India) are induced when the lake level rises faster than 12.2 m per week[10] and, at Nurek reservoir (Tadjikistan), the largest local earthquakes occurred during abrupt decreases in the reservoir filling rate[11]. So the Roselend observations might provide clues as to how, at Koyna and Nurek, loading rate or fluid-flow rate influence the behaviour of brittle, inelastic rock.

How do crustal rocks respond inelastically to loading by a surface reservoir? Although induced stresses and pore pressures vary spatially around a reservoir, they are unlikely to be much greater than 0.1 MPa for each 10 m of water depth. Nonlinear behaviour of rock mass seems to occur at low stress, and must therefore be dominated by deformation of fluid-filled void space, including cracks and faults. One question is whether stress concentration at crack tips allows the creation of new crack surfaces under loads such as those imposed by lakes, which could increase permeability, facilitate radon dissipation and locally weaken the rock mass. Another issue is whether the loading-rate dependence of rock-mass deformation reflects the frictional character of fractures or time delays due to pore-fluid diffusion. Trique and colleagues[1] attribute radon and electric-field anomalies to changing rates of fluid flow in the rock, a hypothesis that could be tested by monitoring groundwater flow near Roselend lake.

More than 20 years ago, earthquake scientists demonstrated that raising and lowering subsurface fluid pressure could turn microearthquakes on and off in Colorado's Rangely Oil Field[12]. Laboratory experiments had already shown that increased pore-fluid pressure counteracts the compressive stress on fault planes in rock, reducing the shear stress required for slip, but it was the Rangely results that really caught seismologists' attention. Large-scale field experiments, such as those carried out by Trique *et al.*, are orders of magnitude closer in size to that of earthquake-producing faults, and they encompass the natural fractures that concentrate deformation and conduct fluid. Work at this scale can determine how radon emission and electric fields are affected by crustal deformation, fluid flow and specific geological structures. And that might clarify their relevance to earthquake prediction. ☐

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1. Trique, M., Richon, P., Perrier, F., Avouac, J. P. & Sabroux, J. C. *Nature* **399,** 137–141 (1999).
2. Wakita, H., Nakamura, Y., Notsu, K., Noguchi, M. & Asada, T. *Science* **207,** 882–883 (1980).
3. Varotsos, P., Alexopoulos, K., Lazaridou-Varotsou, M. & Nagao, T. *Tectonophysics* **224,** 269–288 (1993).
4. Stuart, W. D. & Tullis, T. E. *J. Geophys. Res.* **100,** 24079–24099 (1995).
5. Gladwin, M. T., Gwyther, R. L., Higbie, J. W. & Hart, R. H. G. *Geophys. Res. Lett.* **18,** 1377–1380 (1991).
6. Roeloffs, E. & Quilty, E. *Pure Appl. Geophys.* **149,** 21–60 (1997).
7. Committee on Fracture Characterization and Fluid Flow *Rock Fractures and Fluid Flow: Contemporary Understanding and Applications* (National Acad. Press, Washington DC, 1996).
8. Jouniaux, L. & Pozzi, J.-P. *J. Geophys. Res.* **100,** 10197–10209 (1995).
9. Silver, P. G. & Wakita, H. *Science* **273,** 77–78 (1996).
10. Gupta, H. K. *Bull. Seismol. Soc. Am.* **73,** 679–682 (1983).
11. Simpson, D. W. & Negmatullaev, S. K. *Bull. Seismol. Soc. Am.* **71,** 1561–1586 (1981).
12. Raleigh, C. B., Healy, J. H. & Bredehoeft, J. D. *Science* **191,** 1230–1237 (1976).

Cell signalling

Calmodulin at the channel gate

Michael D. Ehlers and George J. Augustine

Of all the channels that conduct ions in response to voltage changes across cell membranes, those that carry calcium merit special attention. The Ca^{2+} that enters through these channels acts as a messenger for a host of intracellular signalling events, including feedback processes that regulate activity of the channel itself. Such feedback includes inactivation[1], which closes the channel, and facilitation[2], which enhances channel opening. A number of studies[3–6], including reports by Lee *et al.*[3] and Zühlke *et al.*[4] (pages 155 and 159 of this issue), have now reached the surprising conclusion that calmodulin, which is the classical Ca^{2+} receptor protein inside cells[7], mediates *both* inactivation[3–6] and facilitation[3,4].

Most of the new studies focused on the L-type Ca^{2+} channel, which is involved in contraction of heart muscle, gene expression in neurons, and hormone secretion. The first hint that calmodulin might be involved in Ca^{2+}-dependent regulation of these channels was the observation that deleting part of the channel's cytoplasmic tail prevents inactivation[8]. This deleted region includes a sequence of amino acids that resembles an isoleucine–glutamine (IQ) motif, a domain which, in many other proteins, binds calmodulin.

Four new findings support the idea that calmodulin regulates the properties of Ca^{2+} channels, and that it does so by binding to the IQ-like motif. First, Zühlke *et al.*[4] and Peterson *et al.*[6] show that mutant forms of calmodulin, which cannot bind Ca^{2+}, act as dominant-negative inhibitors of Ca^{2+}-channel inactivation. Although this finding establishes that calmodulin helps to inactivate Ca^{2+} channels, it does not indicate where calmodulin acts. Calmodulin could, for example, bind directly to the channel, or it may have other targets, such as protein

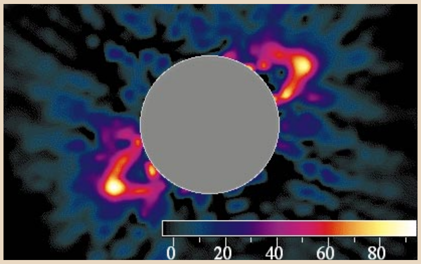
Astrophysics

The planet factory

The first near-infrared image of a dust ring around a young, nearby star has been taken by the Near Infrared Camera and Multi-Object Spectrometer (NICMOS) on board the Hubble Space Telescope. The image may give astronomer Glenn Schneider and his colleagues a new look at early planet formation (*Astrophys. J.* 513, L127– L130; 1999).

Planets are thought to condense out of the disks of dust and gas surrounding newborn stars by a process of accretion— in which small particles collide and stick together. Such circumstellar disks are hard to see, because the glare from the central star outshines the weaker, reflected light from the disk. This particular image was captured using a coronagraphic camera on NICMOS to block out the glare of the star (grey circle on the image).

This disk is unusual as it is only 1.6 billion miles wide (the ring diameter is 13 billion miles), leaving a large dust-free area inside the ring. The much smaller rings found around planets such as Saturn are



held in place by the gravitational force of moons orbiting nearby. The narrowness of this stellar ring implies that it may be confined by one or more unseen bodies — probably new planets. Without some mechanism to keep them intact, dust rings around stars would spread outwards, reducing their ability to form planets.

The colour of the ring is somewhat reddish (scale bar gives flux density in μJy per pixel), showing that it is made up of grains several μm in size, which is larger than typical interstellar dust. This stellar ring is surprisingly young, indicating that planets may have formed in less than ten million years.

Sarah Tomlin