in the fly *Calliphora vicina* adapts its response when the variance of motion signals suddenly changes. Previous studies showed that after neurons have adapted to a change in variance, information transmission — that is, the ability to discriminate among stimuli — is optimized to the new conditions[4,5]. Fairhall *et al.* find that the neuron adapts its input–output relationship extremely rapidly, achieving optimal information transfer within tens of milliseconds. The authors demonstrate that this is about as soon as any system could reliably know that the stimulus distribution has indeed changed.

On the other hand, as mentioned above, firing rate adapts much more slowly, over several seconds. So this cannot be the main mechanism by which information transfer is optimized. Instead, the authors show that the speed of firing-rate adaptation scales to match the frequency of context changes. That is, the dynamics of firing-rate adaptation depend not only on the variance of the preceding and following stimuli, as described above, but also on the 'metastatistic' of how frequently the stimulus conditions change. This suggests that the brain could use the speed of firing-rate adaptation to predict how soon conditions are likely to change again.

Adaptation has a potential drawback, however: if a sensory neuron changes its input–output relationship without notifying the brain that it is operating in a new context, its messages will become ambiguous. In some systems this might not matter, because information about the context would be biologically useless[6]. But Fairhall *et al.* find that, in their system, information about context is not lost as a result of adaptation. Some firing statistics adapt to carry reliable information about the context (variance). These signals could be used to indicate which input–output relationship is operating, thereby removing any ambiguity arising from the shifting response properties of the neuron.

Fairhall *et al.*'s study[1] shows that many independent adaptation mechanisms occur, over a continuous range of timescales. Of course, this raises questions about the mechanisms underlying sensory adaptation. Different forms of adaptation could theoretically be implemented at different levels of organization, ranging from molecules to cells to neural networks. But the authors provocatively speculate that all the observed timescales might be mapped to different biophysical properties of sodium channels. Finally, it is often argued that the coding properties of sensory neurons are adapted to represent their natural stimuli efficiently. Such arguments need to consider that this adaptation may not be hard-wired but rather a dynamic process that occurs throughout the life of an organism. ■

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Earth science

Journey beneath southern Africa

Suzanne Y. O'Reilly

Seismic analyses of the lithosphere, undertaken as part of the Kaapvaal project, provide an unprecedented view of cratons — the earliest parts of continental landmasses.

How continents formed on the early Earth is one of the big questions in geoscience. One way to tackle it is by studying cratons. These are the nuclei of continents that formed during Archaean times, at least 2.5 billion years ago. Southern Africa is an especially rich area of study, so it was the setting for the Kaapvaal project. This international and multidisciplinary programme was designed to probe the architecture and age of the region's lithosphere (the upper mantle and crust that constitute the upper 200–300 km of the Earth). The result, as described in papers in *Geophysical Research Letters*[1–7], is the most detailed picture yet of cratons.

Southern Africa is made up of several terrains ranging in age from Archaean to very young. One of the main sources of information about what is happening deep in the lithosphere is xenoliths — fragments of mantle rock that were carried to the surface in molten rocks called kimberlite magmas. Analyses of xenoliths that erupted through the lithosphere from 1.2 billion to 80 million years ago have allowed measurement of the ages (using a system based on the ratio of rhenium and osmium isotopes)[1,2] and physical properties[3] of the deep Earth beneath southern Africa at the times of eruption.

The most remarkable results of the pro-

100 YEARS AGO

The very remarkable description of the "Fire Walk" collected by Mr. Andrew Lang and others had aroused a curiosity in me to witness the original ceremony, which I have lately been able to gratify in a visit to Tahiti. I had heard that it was performed in Tahiti in 1897, and several persons there assured me of their having seen it, and one of them of his having walked through the fire himself under the guidance of the priest, Papa-Ita… who had also performed the rite at the island of Hawaii some time in the present year, of which circumstantial newspaper accounts were given… According to these, a pit was dug in which large stones were heated *red hot* by a fire which had been burning many hours. The upper stones were pushed away just before the ceremony, so as to leave the lower stones to tread upon, and over these, "glowing red hot" (according to the newspaper accounts), Papa-Ita had walked with naked feet… I could not doubt that if all these were verified by my own observation, it would mean nothing less to me than a departure from the customary order of Nature, and something very well worth seeing indeed.

From *Nature* 22 August 1901.

50 YEARS AGO

Many of the small plankton animals in the sea which are important as the food of fish such as herring, sprat and mackerel swim upwards towards the surface in the evening and down again to deeper levels after dawn. It is of interest from a purely biological point of view to find out what are the factors which govern these movements, and may also be useful in reaching a better understanding of the shoaling of herring. The plankton consist of small animals of many different kinds, small jellyfish, worms and molluscs, hosts of small crustaceans and many others; they nearly all show this nightly vertical migration upwards. Since it has been developed in so many different groups of animals and must use up so much energy every day — some of them climbing more than a hundred feet — it must clearly be of profound significance in their lives. We do not yet understand its meaning and are still only in the stages of studying the actual movements of the animals in relation to different conditions of light, temperature, pressure, etc.

From *Nature* 25 August 1951.

ject came from the deployment of 55 seismometers, which captured information from natural seismic events occurring around the world from April 1997 to July 1999. These data have been used to produce dramatic three-dimensional images of the present distribution of seismic velocity contrasts (Fig. 1). Such contrasts can be used to obtain a picture of the deep structure in the mantle. James *et al.*[4] have identified high-velocity mantle structures, with seemingly irregular lower surfaces, beneath the Kaapvaal and Zimbabwe cratons and the Limpopo belt (Fig. 1). These structures extend to depths of 250–300 km, and are the buoyant roots of cratons that tend to stabilize them against tectonic activity and keep them in one piece. By contrast, mantle beneath the younger fold belts to the south of the cratons is of lower velocity, and probably contains more iron. If the rugged lower surface of the high-velocity volumes is real, it may reflect chemical erosion (by upwelling fluids) of the mantle formed in the Archaean.

The results of the seismic tomography are also valuable in cross-checking inferences drawn from other techniques. Previous estimates of the greatest depth to the base of the lithosphere beneath the Kaapvaal craton lay in the range 200–230 km, and were based on analysis of mantle xenoliths[8,9]. Those estimates are probably within the bounds of error of the seismic and xenolith data: the volcanic action that takes the inclusions to the surface does not necessarily 'sample' the lithospheric column reliably, and the tomography shows large variations in lithosphere thickness over short lateral distances.

The tomography also reveals a region of relatively low seismic velocity across the north of the Kaapvaal craton. This anomaly underlies the Bushveld intrusion, which was formed around 2 billion years ago by the upwelling of more than 455,000 km^3 of mantle-derived magma and extends westward towards the related but unexposed Molopo Farm intrusion. The results confirm previous assumptions that intrusion of huge magma volumes into the crust has affected the whole lithosphere. Mantle of lower velocity can indicate material that is at a higher temperature than its surroundings. Here, however, it probably reflects modification of the mantle by fluids, which has resulted in iron enrichment and a consequent decrease in seismic velocity and an increase in density[9].

Other analyses of seismic data[5] tell us something about the Mohorovičić discontinuity — the seismic boundary between crust and mantle — beneath southern Africa. Above the high-velocity regions it is sharp and relatively shallow (35–40 km); but beneath the Bushveld intrusion and areas of younger crust it is deeper (45–50 km) with a much less defined boundary. This difference could indicate that processes of crustal formation were different in Archaean and post-Archaean times. Or it could be that more complex crust–mantle boundaries are produced by later magmatic or tectonic modification.

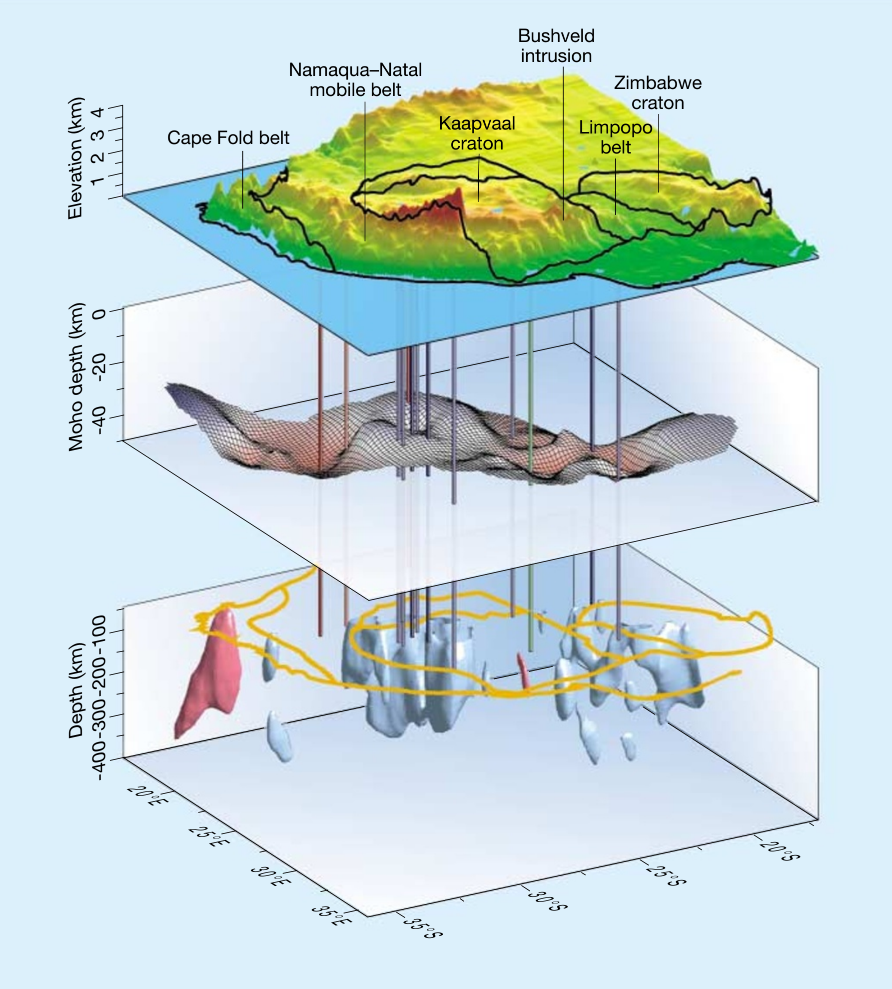

Figure 1 **Summary of the results of the Kaapvaal project. Top, the topography and principal geological boundaries (black lines) in southern Africa. Vertical lines connect the surface outcrop of some kimberlite magmas to the deep features revealed by interpretation of the seismic data (blue lines, 2.5 Gyr; green, 2–2.5 Gyr; red, < 2 Gyr). Centre, the varying depth of the Mohorovičić discontinuity (Moho), which marks the transition between rock types of the crust and those of the mantle. Blue areas indicate the sharp, relatively shallow boundary that exists beneath the cratons; red areas show the deeper and more complex Moho beneath regions where the mantle has been modified by heating or tectonic activity. Bottom, cratonic cores (blue) reveal themselves as regions of high seismic velocity lying beneath the Kaapvaal and Zimbabwe cratons and the Limpopo belt. Regions of lower velocity (red) underlie the southern fold belts and the Bushveld complex, which consists of a huge magmatic intrusion. The yellow outline shows the surface geological boundaries. (Image by M. Fouch and D. James; see ref. 12.)**

Three of the new papers[3,6,7] describe the integration of different ways of defining the seismic anisotropy of mantle beneath southern Africa. Such studies are significant because they may provide evidence of the deformation that has affected different tectonic regions at different times. The Archaean mantle of cratons shows weaker anisotropy than the adjacent, younger regions. Overall, the authors conclude that the Archaean did not have the large-scale regional fabrics (the 'grain' of deformational features) associated with the convergent tectonics that characterized later times.

A crucial part of the puzzle in this research is dating the time of lithosphere stabilization — that is, when the crust and the mantle became welded together. The conclusion[1] from whole-rock rhenium–osmium dating of xenoliths is that the south-eastern Kaapvaal craton was stabilized about 2.8 billion years ago. This age is similar to that inferred for xenoliths from the lower crust, and is within the range of previous data on xenoliths from the Kaapvaal mantle[10]. However, the *in situ* rhenium–osmium analysis of sulphide minerals in such xenoliths[11] has shown that a single xenolith may contain several generations of sulphides, resulting in mixed ages. In the future, this *in situ* approach may provide more precise ages for lithosphere stabilization, and may distinguish stabilization from later events of crust–mantle disturbance, such as the vertical migration of melts.

Another piece of the puzzle for reconstructing craton formation has come from xenoliths of basalt composition called eclogites, which form a small percentage of the mantle and contain some types of diamonds[2]. These eclogites (and their diamonds) are thought to have formed after craton stabilization, either by intrusion of magmas or by recycling into the mantle of basaltic crust that formed earlier. The stable isotope compositions (including carbon and oxygen) of these eclogite xenoliths support a recycled origin, as the values obtained are similar to those in altered basalts from the sea floor. However, rhenium–osmium ages for the formation of these eclogites are about 500 million years older than the (presumably) surrounding mantle rocks[1]. This surprising result may be an artefact of the analytical technique, which may give mixed ages for mantle rocks rather than the age of their original formation, as mentioned above.

There is much speculation about how cratons formed and evolved. A commonly held view is that the processes operating deep in the Earth to form the lithosphere in Archaean times were fundamentally different from those forming the lithosphere today. The Earth's mantle was much hotter in the Archaean, and this caused large-scale melting, with relatively iron-rich magmas adding to the crust and the complementary magnesium-rich residue forming the buoyant mantle layer of the Archaean lithosphere. There is evidence[9] from distinctive layered mantle lithosphere in some cratons that large mantle plumes (upwelling blobs of very hot, deep mantle material) provided not only the source of heat for this melting, but also the material that separated into the magmas and residue that formed Archaean cratons.

The Kaapvaal project has provided an unprecedented seismic context for xenolith studies of cratons in southern Africa. Such a context is needed to complement the understanding gleaned from xenoliths in other cratonic regions, such as Siberia, and in the Slave Craton in Canada. ■

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Developmental biology

Clocks and Hox

Clifford J. Tabin and Randy L. Johnson

Segmentation is a key feature of many animals. New molecular studies add to our understanding of how vertebrate segments form and how this process is linked to the genes that make each segment unique.

In vertebrates, the spine, ribcage and breastbone are derived from repeated blocks of tissue that begin as identical units in early development and are then modified into unique shapes with different purposes. Some segments, for example, allow the head to move; some are sites of attachment for the muscles involved in breathing; and some protect the organs in the chest. To produce such a body plan, there must be mechanisms both for generating the segments and for giving each its distinct identity. For vertebrates, the task of producing repeated units seems to be controlled partly by a molecular clock in the unsegmented paraxial mesoderm — the tissue from which the units arise. The identity of the units is controlled by the differential expression of genes known as Hox genes in a nested pattern from the head to the tail[1]. Writing in *Cell*, Dubrulle *et al.*[2] and Zákány *et al.*[3] suggest that these processes are causally connected.

Simply put, segmentation in vertebrate embryos occurs as follows. On each side of the neural tube (which forms the spinal cord) is a strip of unsegmented ('presomitic') mesoderm. Cells from this tissue progressively bud off, contributing to somites — the units of cells that will later develop into vertebrae and associated muscles. This differentiation process occurs in a wave that moves gradually from the head to the tail (that is, down the anterior–posterior axis), with presomitic mesoderm in front of the wave and somites in its wake.

The molecular and genetic mechanisms that control vertebrate segmentation are not yet understood, but emerging evidence supports a long-standing theory known as the 'clock-and-wavefront' model[4] (Fig. 1). In this model, an autonomous developmental timer (the segmentation clock) interacts with a molecular wavefront of differentiation, which converts information from the clock into spatial information. The model has received support from the discovery of several genes whose expression patterns oscillate in the presomitic mesoderm with the same periodicity as that of somite formation (reviewed in ref. 5).

Dubrulle *et al.*[2] now provide evidence that the wavefront may correspond to a sharp gradient of fibroblast growth factor-8 (FGF-8) protein within the presomitic mesoderm. Grafting experiments in chick embryos[2] showed that presumptive somites –I to –V (see Fig. 1) are fixed with respect to their anterior–posterior polarity and boundaries. But the tissue posterior to somite –V is not yet fixed in this way. Dubrulle *et al.* show that this 'undetermined' zone of the presomitic mesoderm corresponds to a posterior domain of high FGF-8 expression.

Dubrulle *et al.* also found that widespread, forced expression of FGF-8 is sufficient to keep the cells of the presomitic mesoderm in an immature, undifferentiated state. Moreover, when FGF-8 protein was applied locally to one part of the presomitic mesoderm, a series of small somites formed. However, the total number of somites remained the same, because a larger-than-normal somite developed posterior to the smaller ones. Conversely, when signalling from FGF-8 was blocked, larger somites formed. How can these results be explained?

The authors' detailed observations[2] of oscillating gene expression show that forced FGF-8 signalling does not affect the segmentation clock itself. Rather, their data suggest that an interaction between FGF-8 signalling and the clock controls somite size, possibly by specifying the location of boundaries between presumptive somites. So, the clock determines when the boundaries form, and the gradient of FGF-8 determines where. When more FGF-8 is applied to the embryo, the FGF-8 gradient continues further than normal in the anterior direction, and more presomitic mesodermal cells are prevented from contributing to somites. But each somite is programmed to develop at the same time as usual, so each somite ends up containing fewer cells and is therefore smaller. Conversely, blocking FGF signalling shifts the determination front in the posterior direction, and so more cells are allocated to each somite behind the front. This interpretation is consistent with a role for FGF signalling in mediating the wavefront component of the clock-and-wavefront model (Fig. 1).

Once somites have formed, they must