Stenni *et al.*'s calculations result in two time series of relative temperature change, one for the Antarctic plateau and the other for the moisture source for East Antarctic precipitation. General circulation models and isotopic tracer studies show that this moisture source is the area between 30° and 50°S in the Indian Ocean.

A potential problem remains. The deuterium excess proxy for SST can only tell us about the evaporation temperature of the average moisture reaching Dome C. The SST variations reported by Stenni *et al.* may thus merely reflect changes in the relative contribution of moisture from different latitudes with different mean SSTs. However, this possibility is addressed by the report by Sachs *et al.* on page 2077 (*5*), which should put to rest any remaining skepticism about the utility of deuterium excess.

Sachs *et al.* determine SSTs (*6*) from a sediment core from the southeast Atlantic, at about the same latitude (41°S) as the average moisture source for Dome C. The results are remarkably similar to those of Stenni *et al.* (see the figure). Both show a change of about 4°C across the glacial-interglacial transition and of 2°C between 30,000 and 20,000 years before present. They also generally agree on the magnitude of change (1° to 2°C) for more rapid temperature fluctuations. This provides an independent empirical calibration of deuterium excess versus SST. The effective sensitivity is about 1 per mil per degree Celsius, in excellent agreement with the relation determined from models (*7*, *8*).

What do the two data sets tell us about climate change? Above all, they both show that mid-latitude SSTs parallel neither the classic Southern Hemisphere temperature record (the Vostok ice core) nor the archetypal North Atlantic temperature records (the central Greenland ice cores). The most marked difference, highlighted by Sachs *et al.*, is that when the polar regions cooled between 40,000 and 25,000 years ago, the mid-latitudes (at least in the Southern Hemisphere) experienced warming.

Stenni *et al.*'s data do not cover this period, but published deuterium excess data from Vostok—which can now be interpreted with greater confidence in terms of SST—show the same increasing trend (*7*). This trend parallels local insolation changes that primarily reflect variations in the tilt of Earth's axis, adding support to the hypothesis (*9*) that the growth of Northern Hemisphere ice sheets owes as much to warming of the mid-latitudes (and the resulting increase in poleward moisture transport) as to the cooling of the poles. In that case, neither the polar regions nor the lower latitudes are the dominant players in the ice-age cycle: All latitudes play different but equally important roles.

Another important finding is Stenni *et al.*'s observation of a cold oscillation in Indian Ocean SSTs, about 800 years after the Antarctic Cold Reversal (~14,000 years ago) seen in Antarctic climate records. It remains to be determined whether this "Oceanic Cold Reversal" is a Southern Hemisphere expression of the Younger Dryas cold period in the North Atlantic, with which it is suspiciously comparable in timing. There is no doubt, however, that the Antarctic Cold Reversal precedes the Indian Ocean cooling: Stenni *et al.*'s study neatly avoids relative dating uncertainty (which often plagues paleoclimate studies) because both local Antarctic temperature and distant SST records are derived from a single ice core.

Sachs *et al.*'s data show no Oceanic Cold Reversal but do show a small cooling during the Antarctic Cold Reversal. Taken alone, this appears to confirm earlier work showing an antiphase relation between the Southern and the Northern Hemispheres, which has led to the concept of a temperature "seesaw" between the hemispheres (*10*). Stenni *et al.*'s results suggest otherwise. It seems that the north-south antiphase may be limited to the Atlantic and that the seesaw model is far too simple to account for the real longitudinal and latitudinal heterogeneity of millennial-scale climate change.

Just as interannual variation in modern climate cannot be captured with one or two temperature records, understanding century-scale, millennial-scale, and longer term changes of past climate requires records from across the globe. The unexpected results of the new records demonstrate that this task is still in its infancy.

References and Notes

1. J. Jouzel, *Science* **286**, 910 (1999).
2. M. E. Mann, R. S. Bradley, M. K. Hughes, *Nature* **392**, 779 (1998).
3. L. Merlivat, J. Jouzel, *J. Geophys. Res.* **84**, 5029 (1979).
4. B. Stenni *et al.*, *Science* **293**, 2074 (2001).
5. J. P. Sachs, R. F. Anderson, S. J. Lehman, *Science* **293**, 2077 (2001).
6. The authors use alkenone paleothermometry, in which the ratio of di- and tri-unsaturated 37-carbon methyl ketones in the sediment is measured and converted to SST with an empirical calibration.
7. F. Vimeux *et al.*, *Nature* **398**, 410 (1999).
8. K. M. Cuffey, F. Vimeux, *Nature* **412**, 523 (2001).
9. M. Khodri *et al.*, *Nature* **410**, 570 (2001).
10. T. F. Stocker, *Science* **282**, 61 (1998).

PERSPECTIVES: GEOPHYSICS

Top-Down Tectonics?

Don L. Anderson

There are two competing models for mantle convection. In the first, the mantle is stratified into two or more separate convecting regions. In the second, the whole mantle convects as a single unit. Recent progress in plate tectonics, seismology, solid-state physics, and mantle convection is providing strong support for stratified convection. The results may also help explain how plate tectonics relate to mantle convection. Upper mantle convection may be driven by plate tectonics, whereas the deep mantle may convect in a completely different style.

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Evidence for whole mantle convection comes primarily from seismology (*1*). Images of bright blue bands represent high-velocity seismic anomalies that appear to be slabs traversing the mantle. The visual evidence for occasional slab penetration below 650 km (*2*) is usually taken as sufficient evidence for whole mantle convection. Whole mantle convection is also the reigning paradigm among geodynamic modelers because of the seismic evidence cited above and the similarity between the geoid (the surface of constant gravitational potential that would represent the sea surface if the oceans were not in motion) and deep mantle seismic tomography (which works much like medical x-ray tomography except that seismic velocities are imaged). Whole mantle convection simulations are also easier to do.

Arguments for stratified convection are more complex and harder to understand (*2*, *3*). Pressure suppresses the effect of temperature on density, making it more difficult for the deep mantle to convect. It also suppresses the effect of temperature on seismic velocities, which are used by seismologists to map temperature variations. Ab initio calculations of mantle minerals (*4*, *5*) indicate that subtle differences in seismic gradients and velocities may be compositional; even small changes in chemistry can stratify mantle convection. Furthermore, computer simulations of three-dimensional (3D) mantle convection with self-consistent thermal properties and variable heating (*6*) show thermochemical convection involving deep dense layers, which help explain the spatial and spectral

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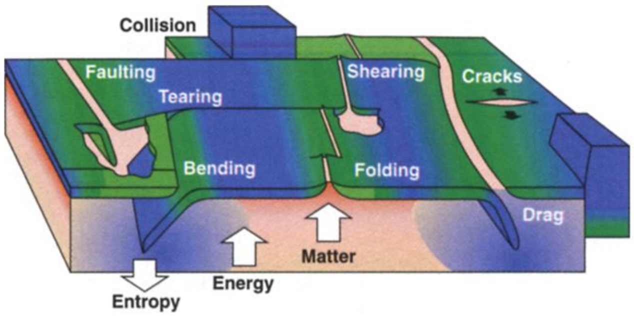


Three ways to flow. (Top) A fluid layer cooled from above or from the side, or heated from within, develops narrow cold downwellings that cool the interior. The downwellings are terminated by phase changes, density increases due to composition, or high viscosity. There are no active or hot upwellings. This resembles the upper mantle. **(Middle)** A high viscosity or isolated chemical layer cooled from above develops large cool downwellings. This mimics the mid-mantle (1000 to 2000 km). **(Bottom)** A deep, dense, high-viscosity layer with low thermal expansion overlying a hot region develops large, sluggish upwellings. This mimics the deep mantle.

features of tomographic models derived from seismic data.

An important measure of the vigor of convection and the distance from static equilibrium is the Rayleigh number, R. The smaller R is, the harder it is for convection to occur. In a spherical shell, convection occurs spontaneously when R is about 10^4 (*7*). Whole mantle convection models usually assume $R > 10^7$, but Tackley (*6*) derives a value of only about 4000 for the base of the mantle. If the lower 1000 km of the mantle is isolated, R drops to 500.

These results have far-reaching implications. Small values of R imply that instabilities forming at the base of the mantle must be sluggish, long-lived, and immense. This is consistent with lower mantle tomography, which has shown that the deep mantle is characterized by two immense regions of low seismic velocity (*8*, *9*), and makes it more plausible than previously thought for the mantle to be chemically stratified. Deep, dense layers need only be a fraction of a percent denser than the overlying layers to be trapped because thermal expansion is low and it is difficult to create buoyancy with available temperature variations and heat sources. The gravitational differentiation of the deep mantle may be irreversible, although mixing, overturn, and penetration may be possible at lower pressure and at an earlier stage of Earth history (*10*).

Equation of state modeling (which captures the equilibrium conditions of a system in terms of pressure, volume, and temperature) has shown that physical differences in the deep mantle, and across chemical interfaces in the mantle, must be very small and almost independent of temperature (*4*, *5*, *11*). What tools can seismologists then use to determine whether the mantle is chemically stratified? Most promising are spectral (*8*, *12*), matched filter (*9*, *13*), scattering, and correlation (*9*) techniques, as well as regional studies (*2*) and anisotropy (*14*). All these techniques support a seismic compartmentalization of the mantle with boundaries near 650 km, ~1000 km, and ~2200 km depth (*9*, *12*, *15*). Visual inspection of tomographic images (*11*) has also been used but has led to opposite conclusions (*2*, *16*).

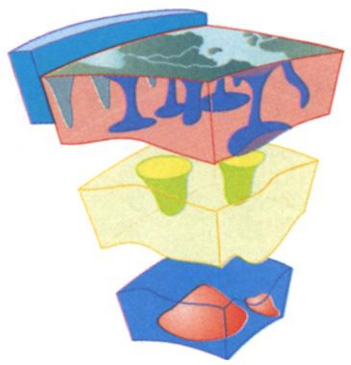
The most prominent seismic discontinuity in the mantle is at 650 km, but the boundary of the lower mantle should probably be placed at 1000 km, as proposed by Bullen and Jeffreys (*2*). Between 650 and 1000 km, steep subduction turns to predominantly horizontal flow; slablike features below 1000 to 1200 km are not connected to surface plates or presently subducting slabs (*2*) and have little correlation with subduction history (*9*). Furthermore, it has been inferred from anisotropy measurements (*14*) that the mantle is divided into two convective systems at 900 to 1000 km.

These inferences are bound to be controversial, but the evidence for a significant geodynamic boundary near 1000 km is as strong, although of a different kind, as the early evidence for other seismic discontinuities in the mantle (*15*). Whether the different mantle regions define independent compositional or convection regimes remains to be seen, but their existence provides constraints that challenge convection models and geochemical assumptions.

How does mantle convection relate to plate tectonics? In 1900, Henri Bénard heated whale oil in a pan and noted a system of hexagonal cells. Lord Rayleigh analyzed this pattern in terms of the instability of a fluid heated from below. Rayleigh-Bénard convection has since become the classic example of thermal convection. In 1958, Pearson (*17*) showed that Bénard's patterns were driven from above by surface tension. Bénard's patterns have also been used as the prototype far-from-equilibrium self-organized dissipative system.

There are several lessons to be learned from these experiments. First, things are not always as they seem. It seemed obvious that the system was driven from below and that the fluid was self-organizing via thermal buoyancy and viscous dissipation of the fluid. Actually, the system was driven and organized from above. Plate tectonics and mantle convection may also be organized and controlled from the top, not by surface tension but by the gravity-controlled compression that defines the plates and plate boundaries. The plates may also control the thermal evolution of the mantle (*18*), with resisting forces in the plates dominating over mantle viscosity.

Second, a far-from-equilibrium dissipative system is sensitive to small internal fluctuations and prone to massive reorganization. Such self-organization requires an open system, a large steady outside source of matter or energy, nonlinear interconnectedness of system components, multiple possible states, and dissipation. Plate tectonics is driven by negative buoyancy of the outer shell and appears to be resisted primarily by dissipation forces in the lithosphere (see the second figure).



Top-down tectonics? The tectonic plates can be viewed as an open, far-from-equilibrium, dissipative and self-organizing system that takes matter and energy from the mantle and converts it to mechanical forces (ridge push, slab pull), which drive the plates. Subducting slabs and cratonic roots cool the mantle and create pressure and temperature gradients, which drive mantle convection. The plate system thus acts as a template to organize mantle convection. In contrast, in the conventional view the lithosphere is simply the surface boundary layer of mantle convection and the mantle is the self-organizing dissipative system.

If most of the buoyancy and dissipation is provided by the plates while the mantle simply provides heat, gravity, matter, and an entropy dump, then plate tectonics is a candidate for a self-organized system, in contrast to being organized by mantle convection or heat from the core. Stress fluctuations in such a system cause global reorganizations without a causative convective event in the mantle. Changes in stress affect plate permeability and can initiate or turn off fractures, dikes, and volcanic chains. The mantle itself need play no active role in plate tectonic "catastrophes."

The difficulty in accounting for plate tectonics with computer simulations may be explained if plates are a self-organized system that organizes mantle convection, rather than vice versa. Upper mantle convection patterns should then be regarded as the result, not the cause, of plate tectonics. Whether the first-order features of plate tectonics emerge from this approach remains to be seen (*19*).

The mantle is usually considered as a homogeneous convecting layer that expresses itself at the surface in plate tectonics. Progress in understanding the base of the mantle, the mid-mantle, and the surface boundary layer show that this is much too simple a view. Theory shows that chemical stratification is difficult to detect with standard techniques. But a stratified mantle, along with the self-regulation of the plates, would slow down the cooling of Earth and postpone the inevitable heat death.

Thermochemical 3D convection simulations in spherical shell geometry and with self-consistent pressure-dependent thermodynamic properties and the possibility of deep undulating chemical interfaces will be required to test these ideas. If plate tectonics is a self-organizing system that also organizes mantle convection, then convection simulations need to allow multiple degrees of freedom so that all possible states can be explored.

References and Notes

1. R. D. van der Hilst *et al.*, *Nature* **386**, 578 (1997).
2. Y. Fukao *et al.*, *Rev. Geophys* **39**, 291 (2001).
3. Tomographic power spectra (*8*) and images (*2*) imply a major change in the flow pattern at 650 km. Matched filtering techniques suggest that the ultimate barrier to subduction is near 1000 km (*9, 13*). Quantum mechanical calculations also suggest stratification and slab trapping near 1000 to 1200 km (*4, 5*).
4. A. R. Oganov *et al.*, *Nature* **411**, 934 (2001).
5. B. B. Karki *et al.*, *Geophys. Res. Lett.* **28**, 2699 (2001).
6. P. Tackley, in *The Core-Mantle Boundary Region*, M. Gurnis *et al.*, Eds. (American Geophysical Union, Washington, DC, 1998).
7. S. Chandrasekhar, *Hydrodynamic and Hydromagnetic Stability* (Dover, Mineola, NY, 1961), p. 654.
8. Y. J. Gu *et al.*, *J. Geophys. Res.* **106**, 11169 (2001).
9. T. Becker, L. Boschi, *Geochem. Geophys. Geosyst*, in press; see www.geophysics.harvard.edu/geodyn/tomography.
10. The deep mantle (below 1000 km depth) has different spatial and spectral characteristics than the upper mantle and may be isolated from it in terms of exchange of material. Density variations of the deep mantle do, however, affect surface elevation, lithospheric stress, and the geoid even if the mantle is chemically stratified. Heat will also flow upwards and may influence the thermal structure, but plate tectonics and subduction may overwhelm this signature because of their shorter time scale.
11. Y. Zhao, D. L. Anderson, *Phys. Earth Planet. Inter.* **85**, 273 (1994).
12. A. Dziewonski, in *Problems in Geophysics for the New Millennium*, E. Boschi *et al.*, Eds. (Editrice Compositori, Bologna, Italy, 2000), pp. 289–349.
13. L. Wen, D. L. Anderson, *Earth Planet. Sci. Lett.* **133**, 185 (1995).
14. J.-P. Montagner, L. Guillot, in *Problems in Geophysics for the New Millennium*, E. Boschi *et al.*, Eds. (Editrice Compostri, Bologna, Italy, 2000), pp. 218–253.
15. The fact that Earth's mantle is split into three or four tomographically distinct regions does not necessarily imply that the mantle is chemically stratified or that the regions are convectively isolated. Phase changes and viscosity variations can also influence the flow. But layered and thermochemical calculations reproduce tomographic features (*6, 16*) and explain the geoid and dynamic topography (*20*). Even features in the deep mantle that have been attributed to slabs have alternative explanations (*16*) consistent with layered convection.
16. H. Cizkova *et al.*, *Geophys. Res. Lett.* **26**, 1501 (1999).
17. J. R. A. Pearson, *J. Fluid Mech.* **4**, 489 (1958).
18. C. P. Conrad, B. H. Hager, *Geophys. Res. Lett.* **26**, 3041 (1999).
19. At equilibrium, the structure that minimizes the free energy is selected. The existence of an equivalent principle for dynamic nonequilibrium systems is an important unsolved problem. The organizing principle for plate tectonics is unknown. Because rocks are weak under tension, the conditions for the existence of a plate probably involve the existence of lateral compressive forces. Plates have been described as rigid but this implies long-term and long-range strength. They are better described as coherent entities organized by stress fields and rheology. The corollary is that volcanic chains and plate boundaries are regions of extension. Plates probably also organize themselves to minimize dissipation.
20. L. Wen, D. L. Anderson, *Earth Planet. Sci. Lett.* **146**, 367 (1997).
21. This paper represents contribution number 8828, Division of Geological and Planetary Sciences, California Institute of Technology. This work has been supported by NSF grant EAR 9726252.

PERSPECTIVES: MOLECULAR BIOLOGY

Turning Gene Regulation on Its Head

Richard Losick and Abraham L. Sonenshein

Gene expression is often thought of as a binary system controlled by a series of on/off switches. New technologies for visualizing genome-wide gene expression reinforce the idea that the state of the cell can be described in terms of the sum total of the on/off states of its genes. In reality, the regulation of gene expression is more subtle. Gene expression can be modulated over a wide range in response to cues from within cells, from other cells, and from the environment. No system better illustrates this fine-tuning than the *trp* operon—the cluster of genes encoding the enzymes that make the amino acid tryptophan—in the Gram-negative bacterium *Escherichia coli*. According to Valbuzzi and Yanofsky (*1*) on page 2057 of this issue, *E. coli*'s elegant bipartite strategy for regulating expression of the *trp* operon is paralleled by an equally elegant but radically different system in the Gram-positive bacterium *Bacillus subtilis*.

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In *E. coli*, the *trp* operon genes are transcribed from a single promoter. The tryptophan produced is loaded onto its specific transfer RNA ($tRNA^{Trp}$) by the enzyme tryptophanyl tRNA synthetase and is then transferred by the $tRNA^{Trp}$ to growing polypeptide chains emanating from ribosomes, the cell's protein synthesis factories. In classic experiments, Yanofsky and co-workers established that *E. coli* regulates transcription of the *trp* operon in two ways: by repressing transcription in response to an increase in the cellular concentration of tryptophan, and by attenuating transcription in response to a rise in uncharged $tRNA^{Trp}$ (that is, $tRNA^{Trp}$ without tryptophan attached) (*2*). At high tryptophan concentrations, the tryptophan repressor protein is activated and it binds to the operon, preventing initiation of transcription; at low tryptophan concentrations, the repressor is unable to bind to DNA, hence RNA polymerase has unfettered access to the operon's promoter and transcription ensues. However, transcription of the *trp* operon is also regulated by sequences located between the 5′ end of the mRNA and the first enzyme coding sequence of the operon. This leader region has domains that can fold into alternative and mutually exclusive stem-loop (hairpin) structures. One stem-loop acts as a transcription terminator, the other as an antiterminator. The leader sequence also includes a tiny coding region containing two tryptophan codons. When tryptophan is abundant, ribosomes are able to move across and translate this short sequence, interfering with antiterminator formation and thereby favoring terminator formation resulting in the termination (attenuation) of transcription. When the cell is starved of tryptophan and the amount of charged $tRNA^{Trp}$ plummets, ribosomes stall at the tryptophan codons in the leader sequence, the antiterminator forms, and terminator formation is blocked. Thus, *E. coli* adjusts transcription of the *trp* operon by relying on two sensors: the repressor, which measures the cellular concentration