

systems that allow us to detect the presence of an eavesdropper by an unexplained increase in error rate. There may well be a valuable consumer product in a few years.

Other possible applications include implementing quantum games (14). Again, security is the key consideration. If you are playing a big-stakes game—such as sealed-bid auctions, digital rights management, or looking for alternatives to taxation for public goods allocation—you want to be sure that the other gamers, or even the system administrator, are not cheating. You may also want to ensure that your move is anonymous, so that it is more difficult for other players to guess your strategy. Quantum computers may offer a way to provide these functions, and, additionally, the inherent randomness of some quantum measurements may be able to enhance fairness.

Whether or not we eventually have quantum security chips in our laptops, the spin-offs from quantum computing research are likely to be at least as exciting. Consider, for example, that single-spin qubits in diamond might be used as ultrasensitive magnetometers operating as nanoscale probes in living cells (15). Other applications include quantum imaging for super-resolution and lensless ghost imaging (16), as well as ultraprecise atomic clocks (17) that can measure general relativistic effects in the universe or at least give us a more accurate global positioning system. Quantum computers are here and are likely to become an important part of our everyday lives in the not-so-distant future.

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## GEOPHYSICS

# The Thickness of Tectonic Plates

Barbara Romanowicz

A fundamental premise of plate tectonics on Earth is that rigid lithospheric plates, formed at mid-ocean ridges, float above a more deformable substratum, the asthenosphere (1). The precise nature of the asthenosphere is still debated. Mechanical models predict a well-defined, sharp lithosphere-asthenosphere boundary (LAB), but evidence for such a boundary from conventional seismic measurements is ambiguous. On pages 499 and 495 of this issue, Kawakatsu *et al.* (2) and Rychert and Shearer (3) present analyses of more sophisticated seismic studies that help refine the LAB and hence the thickness of the lithosphere and tectonic plates, although challenges still remain in picking out this boundary versus other structures within the lithosphere.

Observations of seismic surface waves reveal a well-developed zone where seismic wave velocities are low under the ocean basins, at depths of about 80 to 200 km. This low-velocity zone (LVZ), which also causes strong losses of seismic energy, likely corresponds to the low-viscosity asthenosphere. The thickness of the overlying high-velocity lithospheric “lid” increases with age, which

would be expected as the plates cool after formation. The lithosphere is thickest under the oldest, most stable part of continents, the cratons, and here the asthenosphere is poorly developed. Recent estimates that combine seismic tomography, heat flow, and geochemical data from kimberlites (rocks that originate from the mantle) constrain the lithospheric thickness to about 200 to 250 km under the cratons (4–6).

Other major boundaries in the earth, such as the core-mantle boundary, are more readily observed by seismic body waves that travel through the planet and encounter compositional discontinuities or phase changes. In contrast, detection of the LAB has been elusive, and it has been difficult to determine whether the seismic properties of the LVZ arise from partial melting of rocks (7), from increased water content (8, 9), or simply from the competing effects of increasing temperature and pressure with depth (10).

One approach that has been successful for detecting and characterizing fainter mantle discontinuities is that of “receiver functions” (11), in which conversions of elastic energy from compressional to shear (Ps) or from shear to compressional (Sp) waves are identified on broadband seismic records. This approach constrains the depth, sign, and amplitude of velocity jumps across discontinuities. Receiver function studies have identi-

Seismic studies continue to refine the elusive boundary that defines the depth at which the lithosphere ends.

fied drops in velocity at candidate LABs at depths of about 70 to 80 km under ocean islands (12) and from 80 to 110 km under relatively young parts of continents (13).

Ocean islands, however, generally sit on “anomalous” mantle, such as regions of hotspot plumes. The observation of the LAB under the more representative ocean basins has been hampered by the lack of seismic stations on the ocean floor. The high-quality observations of both Ps and Sp conversions at LAB depths made by Kawakatsu *et al.* were enabled by the long-term operation of several low-noise seismic borehole observatories on the ocean floor in the western Pacific Ocean (14). The sharpness of the LAB boundary rules out a purely thermal origin or one arising only from increased water content. The authors convincingly argue that partially melted rock must be present. This melting process is enhanced by the presence of increased amounts of water at this depth, as was predicted experimentally (15).

The LAB has also been difficult to detect at the expected depths under the cratonic parts of continents (16). Numerous other discontinuities, with either positive or negative jumps in seismic velocity, have been observed at shallower depths and are often referred to as the Hales discontinuity (17). Rychert and Shearer present the results of a global study of Ps receiver functions in vari-

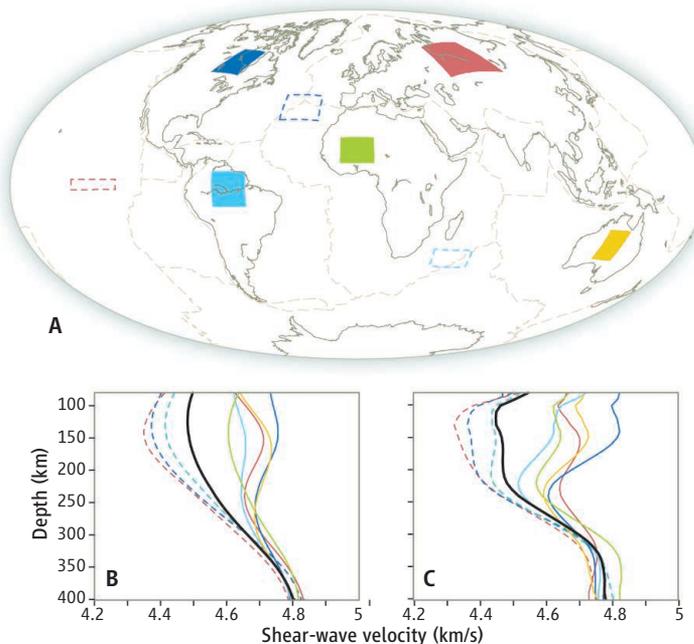
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ous tectonic settings, such as ocean islands, tectonic or stable parts of continents, in which they consistently detect a sharp negative gradient that may correspond to the LAB at a depth that varies surprisingly little between oceanic islands ( $70 \pm 4$  km) and Precambrian shields and platforms that make up continental cratons ( $95 \pm 4$  km). The large velocity drop of shear waves of 6 to 9% indicates that this effect is not caused by changes in temperature or composition alone.

The study of Rychert and Shearer raises several intriguing questions. Is the nature of the discontinuity found by them worldwide and the same everywhere, and is it the same as that found by Kawakatsu *et al.* in the ocean basins? How is the  $\sim 95$ -km discontinuity found under shields and platforms related to the LAB? Why is the expected LAB at depths of about 200 km so hard to detect?

One approach for resolving the different seismic signatures is to make comparisons with the results of high-resolution studies of the continental lithosphere from dense, long-range seismic profiles (LRSPs). These studies consistently find a negative compressional velocity jump at a depth of about 100 km (the so-called “8 degree discontinuity”) (18). At greater depths, the waves are strongly scattered, which suggests that fine layers are present that alternate between high and low velocities. Such a structure could form if heterogeneous inclusions (which could be fluid inclusions) were present (18). These features are likely related to the discontinuity found by Rychert and Shearer as well as to the Hales discontinuity.

The LRSP studies also see features below the 8 degree discontinuity. In shield regions, the LVZ is narrow (10 to 20 km); below it, seismic velocities are faster down to depths of about 200 km. In the younger tectonic parts of continents, the LVZ extends to greater depths. A localized zone of somewhat depressed shear-wave velocities in the cratonic lithosphere is also consistent with



**Shear-wave slowdown.** How seismic shear-wave velocity changes with depth in the upper mantle differs for oceanic and continental regions. Results from two recent global tomographic models illustrate the difficulty in identifying a signature of the lithosphere-asthenosphere boundary. (A) The regions sampled in the profiles are indicated by different colors for continental cratons (solid) and ocean floor (broken lines). Black lines indicate global averages. The global data sets are not identical, but in both cases, they include long-period seismic waveforms sensitive to shear velocity in the upper mantle. The models differ in the initial one-dimensional model used in the linearized inversion. In (B), it is designed to fit the global data on average while keeping variations with depth smooth (26). In (C), it is a mineralogically meaningful (pyrolite) model with more detailed depth variations (27). In both models, velocities are greater under cratons than under oceans down to 200 km depth, and velocity decreases with depth, with a minimum centered at 100 to 150 km under the oceans (similar to results of Kawakatsu *et al.*) and 200 to 250 km in the cratons. In the higher-resolution model (C), a stronger, more localized negative gradient at the base of the cratonic lithosphere is present. A “dip” in velocity occurs at depths around 100 km for both continents and oceans (as seen also by Rychert and Shearer).

some recent tomographic shear-wave velocity models (see the figure). These results suggest that the continental discontinuity seen at about 100 km is not the LAB but more likely the remnant signature of the formation of cratons in archaic times (19).

Although negative velocity jumps at depths of around 100 km under cratons have been attributed to the LAB (20), such conclusions are incompatible with surface wave and teleseismic travel-time data, which tightly constrain the average seismic velocities in the upper mantle. Rather, there seem to be two distinct features: a negative discontinuity with little topography (from 60 to 70 km in tectonic regions to about 100 km under cratons) that is not a mechanical boundary, and a LAB that is not as sharp but has much greater topography, ranging in depth from 60 to 80 km in ocean basins to 200 to 250 km under cratons. Under shields and platforms, the LAB may not be detectable as a disconti-

nuity, because it may extend over a larger depth range and may not involve partial melt but, rather, a change in anisotropy related to the strong shear experienced at the base of the plates. This difference could explain why receiver function studies fail to detect it consistently. Such a scenario is compatible with some LRSP results (21), as well as the observation of a change in the direction of fast axis of azimuthal anisotropy in the velocity of shear waves around the expected depth of the LAB, both in ocean basins (22) and under cratons (23). Under the oceans and under the younger parts of continents, the zones of partial melt and strong seismic anisotropy, because of shear at the base of the lithospheric plates, would overlap, in agreement with Kawakatsu *et al.*'s finding of partial melt zones that are horizontally elongated.

Finally, in the Rychert and Shearer study, only Ps conversions were considered, but in continental settings where the crust is thick, strong multiple reflections from the crust can mask the signal from possible discontinuities at depths around 200 km. The Sp conversion approach does not have this drawback (24). As the Transportable Array component of Earthscope is moved across the Rocky Mountain front and into the North American

shield (25), the combination of surface wave, Ps and Sp receiver function, and other scattered wave field approaches should shed more light on the fine structure of continental roots and their formation, as will similar efforts worldwide. Likewise, further confirmation of the partial melt at the oceanic LAB detected by Kawakatsu *et al.* will require sustained efforts in the installation of broadband ocean floor observatories in oceanic basins.

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## CELL SIGNALING

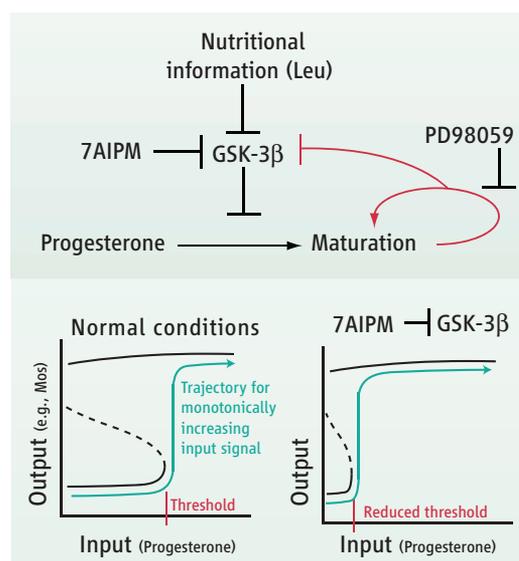
## To Divide or Not to Divide

Jan M. Skotheim

The irreversible decision a cell makes when choosing its fate is based on diverse sources of information. How a cell integrates multiple signals into an all-or-none decision is the fascinating subject of a new study by Justman *et al.* (1) on the maturation of amphibian oocytes in response to the hormone progesterone. On page 509 of this issue, the authors show that interacting feedback loops within the network of cellular signaling pathways modulate sensitivity to progesterone in response to external cues. Depending on the generality of the solution, this work may have broad implications for cellular transitions contingent on multiple signals.

In the frog *Xenopus laevis*, an oocyte arrests cell division (meiosis) and remains quiescent until progesterone triggers its maturation into a fertilizable egg. The hormone rapidly activates signaling pathways that induce the oocyte to resume meiosis. This switchlike response in maturation is based on a positive feedback loop that is activated by the input progesterone signal (2). For an intermediate progesterone input, there is great cell-to-cell variability in the response: Some oocytes proceed through meiosis, whereas others do not respond. Commitment is determined by engagement of the core positive feedback loop (see the figure). Beyond the initiation of positive feedback, removing the activating progesterone signal has no effect, a characteristic of bistable dynamical systems. That is, the system (oocyte) can exist in either of two stable states and transition from one (immature) to the other (mature).

Positive-feedback motifs are found in many genetic and biochemical circuits that control transitions in cellular states. However, positive feedback does not imply bistability. In addition to feedback, bistable systems



**Looped organization.** (Top) GSK-3 $\beta$  forms part of a double-negative feedback loop that modulates the progesterone threshold required to induce positive feedback-driven meiotic maturation in *Xenopus* oocytes. (Bottom) The solid lines indicate the steady-state output for a constant input signal. Two solid lines for the same input indicate hysteresis, i.e., that the eventual steady-state output reflects the time-dependent history of the input.

require nonlinear elements to produce a dramatic threshold response (such as the transition from an immature to mature oocyte). Thus, an input signal (such as progesterone) that exceeds a critical value will rapidly ramp up output, whereas subthreshold signals produce little, if any, response. In the context of oocyte maturation, the mitogen-activated protein kinase (MAPK) signaling cascade is a component of the positive feedback loop that exhibits a nonlinear input-output relationship and is likely to be central to the bistable system response (3).

Although the feedback-driven nature of the dynamical system producing a threshold response to progesterone had been character-

The analysis of signaling circuits governed by threshold-sensitive switches may reveal why a particular network architecture is selected to control a biological process.

ized, it remained unclear whether this response might be modulated to produce a robust output in different environments. Justman *et al.* show that two physiological signals—hormone and nutrient—are integrated into the feedback circuit responsible for oocyte maturation. They also identify a previously uncharacterized, additional double-negative feedback loop that shifts the progesterone threshold in response to environmental conditions.

The molecular link that connects the double-negative loop and raises the progesterone threshold is glycogen synthase kinase-3 $\beta$  (GSK-3 $\beta$ ). Treatment of oocytes with a specific GSK-3 $\beta$  inhibitor [7-azaindoly-pyrazinyl-maleimide (7AIPM)] reduced the progesterone threshold. Similarly, addition of leucine, sufficient to stimulate the target of rapamycin pathway that responds to nutrients (4), also reduced the threshold. Adding both leucine and 7AIPM produced an effect similar to that of 7AIPM acting alone, implying that nutritional information may be transmitted through GSK-3 $\beta$ .

However, GSK-3 $\beta$  may modulate the progesterone threshold through a variety of molecular architectures. For example, the progesterone signal might directly inactivate GSK-3 $\beta$ . To identify the correct regulatory network, Justman *et al.* used PD98059, which inhibits MAPK kinase (MEK), a central component of the positive feedback loop. Adding PD98059 before progesterone stimulation resulted in incomplete GSK-3 $\beta$  inactivation, thereby revealing a substantial effect of feedback on GSK-3 $\beta$  inhibition. Similarly, chemical induction of the feedback loop in the absence of progesterone completely inactivated GSK-3 $\beta$ . Although this work clearly displays the under-

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