Previous studies have implicated adipose tissue and the reproductive system in the regulation of longevity in the fly and the mouse (*3*, *4*, *12–14*). Contrary to the prediction that germline stem cell proliferation is expected to consume most of the energy and to reduce fat storage in *C. elegans*, Wang *et al*. observed that germline stem cell depletion—either by laser ablation of germline stem cell precursors or by a mutation that blocks a pathway that supports stem cell self-renewal (involving the signaling molecule Notch-like receptor GLP-1)—caused the reduction of lipid droplets in intestinal cells where fat normally is stored. On the other hand, overproliferation of germline stem cells—by blocking their differentiation through constitutive GLP-1 signaling—increased fat storage in intestinal cells. This indicates that the germline stem cells directly control fat storage.

Using RNA interference in screens that reduce gene expression, Wang *et al.* identified a triglyceride lipase that, when eliminated, reversed the reduction of fat storage and longevity caused by germline stem cell depletion. Overexpression of the lipase reduced fat storage and extended life span. Further analysis indicated that the lipase regulates fat storage in intestinal cells. These findings indicate that fat metabolism is the missing link between the status of the reproductive system and longevity in the worm. Thus, in response to germline stem cell depletion, the authors propose that somatic cells of the gonad send a signal to reduce fat storage, thereby extending life span.

Previous studies in the worm have also shown that the effects of both the IIS pathway and germline stem cells on longevity require FOXO/DAF-16 (*9*, *11*). As expected, Wang *et al.* observed that disrupting the IIS pathway increased lipase expression in intestinal cells, reduced fat storage, and thus increased worm life span. By contrast, reducing lipase expression partially suppressed longevity caused by a defective IIS pathway. In addition, inactivating FOXO/DAF-16 did not decrease lipase expression nor increase fat storage, but it restored fat storage caused by germline stem cell depletion. Furthermore, although *kri-1* and *daf-12* are important in intestinal cells for activating FOXO/DAF-16 in response to germline stem cell depletion, *kri-1* is required for, whereas *daf-12* is dispensable for, increasing lipase expression and reducing fat storage. These findings indicate that germline stem cell depletion promotes lipid metabolism in intestinal cells by activating a KRI-1–DAF-16 signaling pathway but not the hormone pathway that involves DAF-12. Therefore, the IIS pathway and reproductive signaling converge on FOXO/DAF-16 to control fat metabolism and longevity.

A recent genetic study in *C. elegans* indicates that under the condition of reducing signaling from the IIS pathway below a critical threshold level, the somatic gonad is no longer needed for germline stem cell depletion to extend life span, which suggests that the signals from the reproductive system somehow also impinge on the IIS pathway (*15*). The findings of Wang *et al.* and other studies support a model in which somatic cells of the gonad send signals that impinge on intestinal cells and control two pathways—the KRI-1–DAF-16 pathway and the DAF-12 pathway—to increase longevity (see the figure). The IIS pathway also functions through DAF-16 to control fat metabolism and life span. Signals from germline stem cells block these pathways and shorten life span.

In *C. elegans*, it will be critical to identify the life span–extending signals produced by the reproductive system that act on intestinal cells to control longevity, and to elucidate the molecular details of their effect. Germline stem cell depletion also extends life span in *Drosophila* (*6*), so it is of interest to investigate whether this also involves fat metabolism. Finally, it will be exciting to determine whether germline stem cell depletion can extend life span by regulating fat metabolism in mammals. If fat metabolism is the conserved link between reproduction and aging, we may discover more about how life span is controlled in humans and perhaps find better treatments for age-related diseases.

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GEOPHYSICS

Reconstructing Earth History in Three Dimensions

Bernhard Steinberger

An inverse model elucidates the connection between plate tectonics at Earth's surface and the dynamics of the underlying mantle.

Plate motions at Earth's surface are intimately linked to convective flow in the underlying mantle. These links are becoming more evident through subsurface tomographic images, advances in mineral physics, and improved models of plate motion. Yet, there is still no generally accepted mechanism that consistently explains plate tectonics in the framework of mantle convection. A key obstacle to a better understanding is the fact that, although the configuration of plates at Earth's surface can be reconstructed with some confidence at least back to the Cretaceous, knowledge about the deep interior has been largely limited to the present day. On page 934 of this issue, Liu *et al.* (*1*) point the way to more reliable reconstructions of Earth's past in three dimensions.

The theory of plate tectonics describes how plates move away from each other at spreading ridges, past each other at transform faults, and toward each other at convergent boundaries. In the latter case, one of the plates may get subducted back into Earth's interior. Seismic tomography, which uses travel times between earthquakes and seismographs to construct three-dimensional models of seismic wavespeed distribution of Earth's interior, has yielded images of such subducted "slabs" in ever-increasing detail (*2*). Using subduction inferred from plate reconstructions as input, present-day mantle

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temperature structure can be numerically forward-modeled and the model results compared with the inferred temperature structure based on seismic tomography and mineral physics. By modifying model assumptions, the agreement can be optimized. In this way, forward models have yielded important insights into plate reconstructions and mantle properties (*3*, *4*).

Yet, an obvious drawback of this approach is that it cannot achieve an exact fit between predicted and observed present-day mantle structure. Hence, an alternative approach has been to begin with present-day structure inferred from tomography and compute mantle structure backward in time (*5*). But past mantle structure cannot be completely recovered in this way because information has been lost due to thermal diffusion. At least in the thermal boundary layers at the top and bottom of the mantle, heat transport through thermal diffusion cannot be neglected. However, time-reversing thermal diffusion makes—backward in time—hot material become hotter and cold material colder. Eventually, this effect is bound to create numerical instabilities.

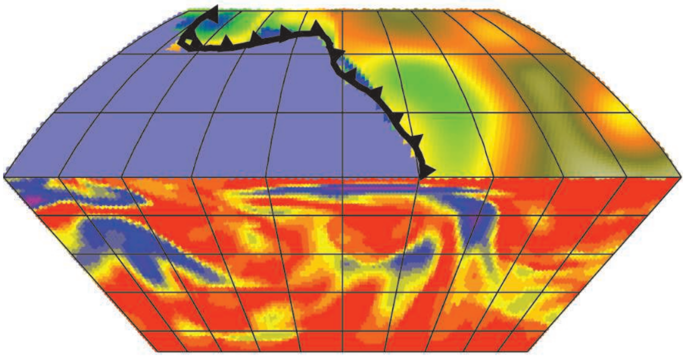
To overcome this problem, inverse approaches to mantle convection have been developed (*6*, *7*), which essentially aim at finding the initial condition, starting from which the forward model optimally recovers the present-day state of the mantle. Solving this problem requires multiple iterations and is computationally intensive. Liu *et al*. now use this approach to obtain a realistic reconstruction of past mantle structure (see the figure).

Plate reconstructions (*8*) provide the surface boundary condition of mantle flow. However, that alone does not guarantee that the reconstruction is geologically reasonable. This is in fact one main problem that Liu *et al*. face: Without modification, the past location of slabs is reconstructed too far east to be compatible with plate reconstructions. The authors overcome this problem by introducing a "stress guide," which essentially allows the Farallon plate (the oceanic plate subducted under the west coast of North America during the past 100 million years) (see the figure) to stuff material sideways under North America. However, it remains unclear how, in the real Earth, such a stress guide could be accomplished, and more generally, how models of the past mantle can be made compatible with plate tectonic reconstructions.

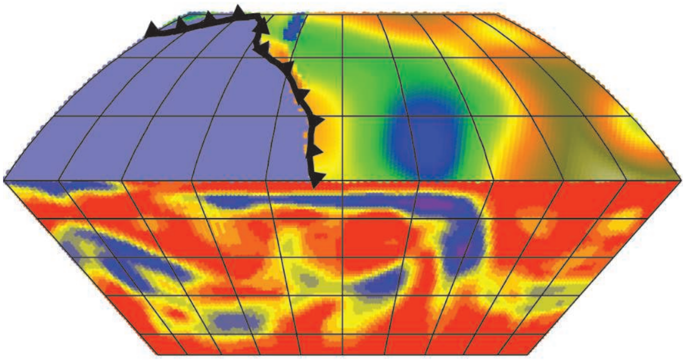
One important aspect of this goal is to devise a common reference frame for plate motions and mantle dynamics (*9*), in particular to distinguish between plate motions relative to the mantle and coherent rotations of the entire Earth relative to its spin axis (true polar wander). Through optimizing agreement between plate tectonic reconstructions of subduction and mantle dynamic reconstructions of slabs, models such as that of Liu *et al*. will be instrumental in finding a common reference frame.

What is all this modeling useful for? Liu *et al*. show one main application: predicting vertical surface motions. Dense material in the mantle causes downward flow and thus pulls down Earth's surface. Hence, when a continent moves over the remnants of a subducted slab, parts of it may get flooded (*10*). Knowing when and where continental flooding has occurred is not merely of academic interest, because the flooding history also influences where sediments and related natural resources may form. Knowledge of uplift and subsidence is also necessary for extracting information about past sea-level change from the geologic record (*5*) and understanding which part of it is caused by ocean basin volume change. It is thus essential for understanding past climates and ultimately helpful for better understanding causes and effects of present climate change.

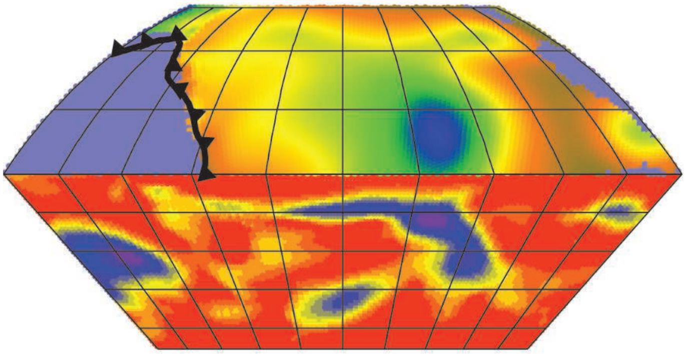
Many challenges remain. Liu *et al*. avoid unnecessary complexity, using simple models of



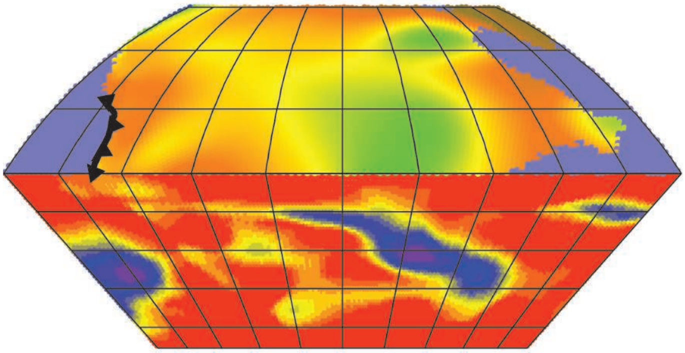
100 million years ago



70 million years ago



40 million years ago



Present day

Going down. Mantle temperature is shown at the front, continental dynamic topography at the top. Ocean floor is subducted along a trench (black line with triangles) at the western edge of North America. The subducted slab (in "cold" colors on the temperature cross section) causes negative topography (green and blue colors on top). The North American plate overrides this topography low, which becomes less pronounced as the slab sinks toward the base of the mantle. All data provided by L. Liu (*1*). The figure was prepared using the GMT (*11*) software.

mantle rheology for relating seismic wave-speed variations to temperature. Future studies will aim at making models gradually more Earth-like. A key aspect of this will be to develop more realistic models of lithospheric strength, which controls the amount of deflection that can develop due to buoyant mantle loads, and drag of the flowing mantle at the base of the lithosphere, which can lead to lithospheric deformation. Improved models of topography development must link mantle dynamics to these more realistic lithosphere models. Toward this goal, the work of Liu *et al*. is a major step in linking plate tectonics and mantle dynamics.

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APPLIED PHYSICS

Plasmonics Applied

Surface plasmons, light-induced excitations of electrons on metal surfaces, may provide integration of electronics and optics on the nanoscale.

Albert Polman

The ability to engineer metal surfaces and particles at the nanoscale has led to the rapid development of the field of "plasmonics," the optical properties of metal structures at the nanoscale. Surface plasmons are optically induced oscillations of the free electrons at the surface of a metal. Electron beam lithography, focused ion beam milling, and self-assembly have provided routes to engineer complex arrays of metal nanostructures in which plasmons can be excited, directed, and manipulated. The attractiveness of plasmons is that they can effectively confine the optical excitation in a nanoscale volume and thus mediate strong optical interactions within this volume. Also, the wavelength at which these phenomena are observed can be tuned by varying the metal shape and dielectric environment, thereby providing a broad palette from which to choose the desired optical properties for an application.

Early work in plasmonics focused on the study of resonances and electromagnetic field enhancements in individual metal nanoparticles and particle assemblies. The plasmon coupling within arrays of metal nanoparticles can lead to the formation of nanoscale hot spots in which the intensity of light from an incident beam can be concentrated by more than four orders of magnitude. This leads to a large improvement in sensing techniques that use optical radiation, such as Raman spectroscopy, with potential applications in medical diagnostics. The effect of light concentration via plasmons is most apparent in phenomena that are nonlinear in light intensity, as demonstrated recently by the on-chip generation of extreme-ultraviolet light by pulsed-laser high harmonic generation (*1*). This opens a wealth of prospects in lithography or imaging at the nanoscale through the use of soft x-rays (see the figure, left panel).

Because the plasmonic interaction between metal nanoparticles is very sensitive to their separation, precise measurements of the plasmon resonance wavelength of metal particle assemblies functionalized with biomolecules can be used as a molecular-scale ruler that operates over a length scale much larger than that in the fluorescence energy transfer metrology that is routinely used in biology (*2*). Practical applications of this concept in systems biology, such as imaging of the motion of molecular motors, are being pursued. Already, measurement of plasmonic resonance shifts is used in the detection of biomolecules (see the figure, middle left panel), and indeed standard commercial pregnancy tests are based on this principle. A potentially far-reaching application is the use of particles composed of a dielectric core and a metallic shell (*3*) in cancer treatment. These particles, when injected into the human body, are selectively bound to malicious cells, whereupon laser irradiation at a precisely engineered plasmon resonance wavelength is used to heat the particles and thereby destroy the cells. Clinical studies are showing promising results (*4*).

Suitably engineered metal nanostructures can also act as antennas in which the resonant coupling between the particles concentrates light into well-defined hot spots (*5*), enabling ultrasmall, wavelength-sensitive directional sensors or detectors. The same metal particle arrays, when coupled to optical emitters, can also act as directional emitters. Indeed, the enhanced optical density of states near the surface of metal nanoparticles can provide control over the color, directionality, and polarization of light-emitting diodes. This concept may find large-scale applications in the areas of solid-state lighting and photovoltaics (see the figure, middle right panel). Calculations and experiments (*6*) show that light scattering from metal nanoparticle arrays placed on top of a thin-film semiconductor layer can effectively fold the path of sunlight into the layer, strongly enhancing its effective absorption.

Parallel to the development of plasmonic structures based on metal nanoparticles, the propagation of plasmons along metal waveguides is also being investigated. Here too, precise control over material and geometry allows the wave-guiding properties to be controlled in ways that cannot be achieved with regular dielectric waveguides. In particular, extremely short wavelengths can be achieved at optical frequencies. It has been shown that light with a free-space wavelength of 651 nm, squeezed in a metal-insulator-metal plasmonic waveguide, has its wavelength shrunk to only 58 nm (*7*). The next challenge will be to shrink it further, into the soft x-ray wavelength regime. Similar to the coupling within nanoparticle assemblies, this effect is due to the coupling between plasmons propagating at the two metal-insulator interfaces. By further tailoring plasmonic waveguide structures, the propagation speed of plasmons can be reduced well below the speed of light (*8*). More complex geometries, in which arrays of nanoholes are integrated in a metal film, act as efficient color filters (*9*). Interestingly, in some geometries, plasmon waveguides exhibit a negative refractive index for the guided plasmon, and indeed two-dimensional negative refraction has been observed in these plasmonic waveguides (*10*).

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