

Another possibility is that the brain's enormous intrinsic functional activity facilitates responses to stimuli. Neurons continuously receive both excitatory and inhibitory inputs. The "balance" of these stimuli determines the responsiveness (or gain) of neurons to correlated inputs and, in so doing, potentially sculpts communication pathways in the brain (4). Balance also manifests at a large systems level. For example, neurologists know that strokes that damage cortical centers that control eye movements lead to deviation of the eyes toward the side of the lesion, implying the preexisting presence of "balance." It may be that in the normal brain, a balance of opposing forces enhances the precision of a wide range of processes. Thus, "balance" might be viewed as a necessary enabling, but costly, element of brain function.

A more expanded view is that intrinsic activity instantiates the maintenance of information for interpreting, responding to, and even predicting environmental demands. In this regard, a useful conceptual framework from theoretical neuroscience posits that the brain operates as a Bayesian inference engine, designed to generate predictions about the future (5). Beginning with a set of "advance" predictions at birth (genes), the brain is then sculpted by worldly experience to represent intrinsically a "best guess" ("priors" in Bayesian parlance) about the environment and, in the case of humans at least, to make predictions about the future (6). It has long been thought that the ability to reflect on the past or contemplate the future has facilitated the development of unique human attributes such as imagination and creativity (7, 8).

fMRI provides one important experimental approach to understanding the nature of the brain's intrinsic functional activity without direct recourse to controlled stimuli and observable behaviors. A prominent feature of fMRI is that the unaveraged signal is quite noisy, prompting researchers to average their data to reduce this "noise" and increase the signals they seek. In doing this, it turns out that a considerable fraction of the variance in the blood oxygen level-dependent (BOLD) signal of fMRI in the frequency range below 0.1 Hz, which reflects fluctuating neural activity, is lost. This activity exhibits striking patterns of coherence within known networks of specific neurons in the human brain in the absence of observable behaviors (see the figure).

Future research should address the cellular events underlying spontaneous fMRI BOLD signal fluctuations. Studies likely will cover a broad range of approaches to the study of spontaneous activity of neurons (9,

10). In this regard, descriptions of slow fluctuations (nominally <0.1 Hz) in neuronal membrane polarization—so-called up and down states—are intriguing (4, 10). Not only does their temporal frequency correspond to that of the spontaneous fluctuations in the fMRI BOLD signal, but their functional consequences may be relevant to an understanding of the variability in task-evoked brain activity as well as behavioral variability in human performance.

William James presciently suggested in 1890 (11) that "Enough has now been said to prove the general law of perception, which is this, that whilst part of what we perceive comes through our senses from the object before us, another part (and it may be the larger part) always comes (in Lazarus's phrase) out of our own head." The brain's energy consumption tells us that the brain is never at rest. The challenge of neuroscience is to understand the functions associated with this energy consumption.

ATMOSPHERE

How Fast Are the Ice Sheets Melting?

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Remote-sensing data suggest that ice sheets currently contribute little to sea-level rise. However, dynamical instabilities in response to climate warming may cause faster ice-mass loss.

If the ice sheets covering Greenland and Antarctica were to melt completely, they would raise sea level by about 65 m. But even a small loss of ice mass from the ice sheets would have a great impact on sea level, particularly on low-lying islands and coastal regions. New satellite observations, including those reported by Luthcke *et al.* on page 1286 of this issue (1), now allow estimates of the mass balances of the ice sheets and their evolution through time.

For the past 3000 years, global sea level has remained stable, but since the end of the 19th century, tide gauges have detected global sea-level rises [~ 1.8 mm/year on average over the past 50 years (2, 3)]. Satellite altimetry data document a rate of ~ 3 mm/year since 1993 (4). However, it remains unclear whether the recent rate increase reflects an accelera-

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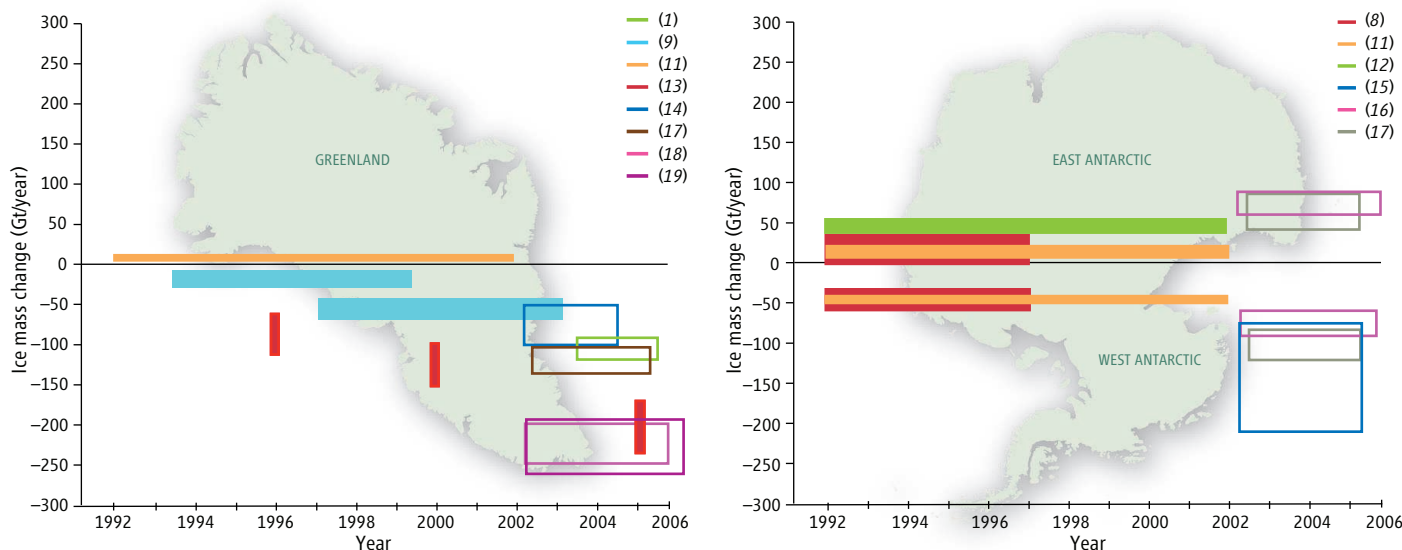
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tion in sea-level rise or a natural fluctuation on a decadal time scale.

Present-day sea-level rise has several causes. During the past decade, ocean warming has contributed roughly half of the observed rate of sea-level rise (5), leaving the other half for ocean-mass increase caused by water exchange with continents, glaciers, and ice sheets (6). The contribution of mountain glaciers and small ice caps to sea-level rise in the past decade is estimated to be ~ 0.8 mm/year (7). These figures constrain the contribution from ice sheets to less than 1 mm/year in the past decade.

Since the early 1990s, remote-sensing data based on airborne laser and satellite radar altimetry, as well as the space-borne Synthetic Aperture Radar Interferometry (InSAR) technique, have provided the first observations of ice sheet mass balance (8–13). These observations indicate accelerated ice-mass loss in recent years in the coastal regions of southern Greenland. In contrast, slight mass gain is reported in central high-elevation regions. Over Antarctica, remote sensing indicates

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Ice-sheet mass change estimated by different remote-sensing techniques. (Left) Greenland. (Right) West and East Antarctica. The ice sheet mass change is given in gigatons per year. The numbers refer to different investigations as quoted in

the reference list. Open bars correspond to GRACE results, filled bars to results from other techniques. The estimate from (15) is an average over the whole of Antarctica. On the right, positive values are for East Antarctica and negative values for West.

accelerated mass loss in the western part of the continent (10), whereas the eastern part is gaining some mass as a result of increased precipitation (11, 12).

Because of these contrasting behaviors—mass loss in coastal regions and mass gain in elevated central regions—ice-sheet mass loss exceeds mass gain only slightly. Thus, according to the recent mass-balance estimates, the ice sheets presently contribute little to sea-level rise. However, great uncertainty remains, mainly because of incomplete coverage by remote-sensing surveys, spatial and temporal undersampling, measurement errors, and perturbation from unrelated signals. In addition, each technique has its biases. For example, radar altimetry misses narrow coastal glaciers because of inadequate ground resolution, and ice elevations measured by the radar are much less reliable over steep, undulated surfaces than over flat high-elevation surfaces. Another uncertainty arises because conversion of elevation change to mass change requires assumptions about the surface density of snow or ice to be made.

Since 2002, the NASA/DLR Gravity Recovery and Climate Experiment (GRACE) satellite mission has provided a new tool for precise measurements of ice-sheet mass balance, with nearly complete coverage of the high-latitude regions up to 89°N/S. GRACE measures the spatiotemporal change of Earth's gravity field. Over the ice sheets, this change can be converted into ice-mass change, assuming that the gravity change results from a change in surface mass.

Several studies have reported estimates of Greenland and Antarctica ice-mass change from GRACE (14–19). The GRACE results

confirm those from other remote-sensing techniques, that is, net ice-mass loss from Greenland and West Antarctica and a slight ice-mass gain over East Antarctica (see the figure). The GRACE results over Greenland also suggest accelerated ice-mass loss since 2002, in agreement with InSAR results (13).

However, the GRACE-based mass-balance estimates are highly scattered (see the figure). One reason is the short time span of the analyses (2 to 4 years, depending on the study). Over Greenland, ice mass varies widely from year to year. Because the analyses do not overlap exactly in time, different trend estimates are to be expected.

Another cause of scatter is contamination from geodynamic processes related to Earth's response to ice melt from the last deglaciation. This effect, which depends on poorly known parameters, is mainly available from modeling, with important differences between models. Moreover, over Antarctica, this effect is of the same order of magnitude as present-day ice-mass change.

A third source of uncertainty is the coarse resolution (400 to 600 km) of most GRACE results (14–19). As a result, the estimated ice-sheet mass change includes contributions not only from small isolated glaciers in the vicinity of the ice sheets, but also from other gravity signals (of oceanic, hydrologic, and tidal origin) from surrounding regions. These perturbing signals are still poorly known, and therefore difficult to be corrected for.

To improve the GRACE resolution, Luthcke *et al.* have applied a new approach over Greenland: They determined mass concentrations at a local scale from appropriate processing of the GRACE observations. This

approach differs from the standard method, in which global solutions of the time-varying gravity field are computed, and a regional filter is then applied to extract the mass signal over the area of interest. The new approach minimizes the contamination from signals unrelated to the ice-sheet mass balance and provides results of finer resolution.

Luthcke *et al.* computed ice-mass change in six drainage basins of the Greenland ice sheet, ranging from coastal low-elevation to central elevated regions. They find ice-mass increase in high-elevation regions of northern Greenland, as suggested by satellite altimetry (11), and ice depletion at the margins of southern Greenland, in agreement with InSAR-based glacier discharge estimates (13). The results confirm accelerated ice flow in coastal regions of southeast Greenland. However, the trend is smaller than reported by some other recent GRACE-based studies (18, 19). Over the 2-year period of investigation, Luthcke *et al.*'s estimate of Greenland's contribution to sea-level rise amounts to ~0.3 mm/year.

However, further research is needed to improve estimates of Greenland and Antarctica mass balance (see the figure) and their contribution to sea level. Besides extending the time series of observations and reducing internal errors, it is important to reconcile estimates from different techniques and to eventually use them in synergy.

The greatest uncertainty in sea-level projections is the future behavior of the ice sheets. In recent years, the velocities of outlet glaciers in coastal regions of Greenland and Antarctica have accelerated, showing that a large fraction of ice-mass loss occurs through dynamical processes

rather than surface melting (9, 10, 13). The dynamical response of the ice sheets to present-day climate forcing may thus play a much larger role than previously assumed. Future dynamical instabilities of the ice sheets is of major concern, given their potential impact on sea level (20), yet comprehensive modeling of such dynamical effects is in its infancy.

Improved mass-balance estimates from remote-sensing observations, such as those reported by Luthcke *et al.*, will inform on the ongoing behavior of the ice sheets and help to validate models. This goal requires long time series of satellite observations,

and hence continuity of space missions.

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PLANT SCIENCE

Distributing Nutrition

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Hunger claims the lives of 20,000 children a day. Worldwide, one of every three children is underweight and malnourished (1). Eradication of malnutrition and associated childhood mortality is a major mission of the United Nations Millennium Development Goals and will require a shared vision of conservation as well as improvements in agriculture that include increasing the nutritional value of staple crops (2). Advances in basic plant sciences applied to agriculture will be critical for success (3). Strong endorsement of this idea comes from two studies on pages 1295 and 1298 of this issue that provide insight into the mechanisms of nutrient distribution in plants (4, 5). This work reminds us that any effort to enrich the nutritional content of plants requires knowledge of the mechanisms of acquisition and distribution of these nutrients throughout the component parts of the crops that are the dietary staple.

Kim *et al.* (4) combine mutational analysis and imaging to demonstrate an essential role for iron in seedling development—specifically, iron localized to an intracellular compartment called the vacuole in the model plant *Arabidopsis thaliana*. Although abundant, iron is relatively insoluble, and the challenge for all organisms is to acquire adequate amounts while avoiding toxicity (6). Iron is essential for oxygen transport throughout an organism and for cellular (mitochondrial) res-



Dietary crops. A market, or *tianguis*, in Huauchinango, Mexico, with indigenous Mexicans and typical crop-based diets.

piration. Iron deficiency is common, affecting 500 million children in populations with crop-based diets. Infants are at greatest risk because brain growth can quickly outpace dietary availability, resulting in long-term neurocognitive impairment (7). Understanding iron homeostasis in plants is therefore essential to any effort intended to increase the iron content of staple foods as an approach to preventing iron deficiency.

In most organisms, iron that is stored in cells is bound to ferritin, a cytoplasmic protein. Unlike humans, but similar to yeast, plant cells contain vacuoles that function as reservoirs for ions and metabolites and could also serve as sites of iron storage (8). Kim *et al.* identify VIT1 as the *Arabidopsis* ortholog of a vacuolar iron transporter, CCC1, previously

New insights into how plants store and mobilize nutrients, such as iron, can help in the fight against world hunger.

identified in yeast. They show that this protein rescues the iron-sensitive phenotype of a yeast mutant that lacks CCC1, mediates iron sequestration into yeast vacuoles, and is highly expressed in developing seeds—an important food source worldwide. However, there is no difference in the total iron content of seeds or shoots between wild-type *Arabidopsis* plants and mutant plants that lack the gene encoding VIT1 (*vit1*). So is VIT1 required for plant iron homeostasis?

In an imaging tour de force, Kim *et al.* use x-ray fluorescence microtomography to demonstrate a dramatic loss of iron in germinating seeds that lack VIT1, specifically in provascular cells of the hypocotyl, radicle, and cotyledon embryonic seed tissues. This finding implicates the vacuole of provascular cells as critical to iron storage in wild-type seeds. Consistent with this idea, *vit1* seedlings germinate poorly under conditions that limit iron availability from the soil. These findings highlight the need to understand nutrient distribution in assessing homeostasis, as well as the importance of noninvasive, three-dimensional quantitative element analysis in living samples. Such approaches will find broad application to issues of nutrient homeostasis in living organisms.

In a related study, Uauy *et al.* (5) characterize *Gpc-B1* from wild emmer wheat as a simple Mendelian quantitative trait locus (genomic DNA that is associated with a particular trait that varies continuously across a population) that is associated with accelerated senescence and increases in grain zinc, iron, and protein content. This wheat is ancestral to

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