

emitted the spikes. The code preserving the greatest amount of information from a population of these neurons uses temporal information taken from the spikes of the neuron emitting them.

These results raise the question of how the brain recognizes spikes from individual neurons. In order for input neurons receiving the spikes to be able to identify which output neuron emitted the spikes, there must be appropriate connections between the two sets of neurons. It is the flow of information across these connections that accounts for much of neural information processing. Thus, it is important to know whether the connections among nearby neurons are segregated (presumably from genetic specification or learning) to preserve the information coming from individual neurons. Jacobs and Theunissen (11) have shown in crickets that the distribution of input neuronal information is weighted according to the placement and numbers of

synapses available to modify incoming signals, in this way yielding efficient modification of information with little redundancy among output neurons.

Recently, large-scale recording techniques have emerged as important tools for identifying brain regions that become activated during execution of a particular task. Such techniques include multiunit recording, which records spikes from several neurons simultaneously with a single electrode regardless of which neuron emitted which spike (see the figure, part C); field-potential recording, which records the total electric field (not just the spikes) at a coarse time resolution in a local region that may represent input or presynaptic signals; and functional imaging, which records a signal related to some metabolic marker such as blood flow that varies relatively slowly over time. The Reich *et al.* results show that it remains critical to study physiological and anatomical data

from sets of individual neurons to learn how local information processing occurs and how modification of this information takes place as signals pass through different processing stages.

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PERSPECTIVES: ARCHAEOLOGY

A New Twist in the Radiocarbon Tale

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Radiocarbon (^{14}C) is generated in the atmosphere by cosmic rays. Its decay is widely used to date organic materials in archaeological and paleoclimate records. But radiocarbon ages can give a warped perspective of time. Without calibration to data sets with known ages, they may deviate from calendar time by up to a few thousand years at the time of the Last Glacial Maximum (about 21,000 years ago). Much effort has been invested in generating long, precise records with known ages to calibrate radiocarbon ages.

It has been assumed that for any given time period the radiocarbon concentration of the atmosphere is the same throughout each hemisphere within the error of measurement. Combined Northern Hemisphere data sets have therefore been used to calibrate radiocarbon ages of samples throughout the hemisphere (1). A few studies have identified ^{14}C differences between various Northern Hemisphere locations (1–3). However, the uncertainty in measurement differences between laboratories can mask small regional offsets. Intralaboratory comparisons between regions have previously only covered

relatively short time periods. A general circulation model found only small offsets within hemispheres at mid-latitudes (4).



Dating archaeological monuments. The biggest of the many Gordion tombs (top) is some 300 m in diameter and about 67 m high. It is entirely manmade. (Right) Remains of the wooden burial chamber inside the mound. This structure is the oldest known wooden building that is still standing, albeit with the help of some modern steel posts and wooden supports. The logs were up to 918 years old at the time they were cut. Manning *et al.* show that they were felled in about 740 B.C.



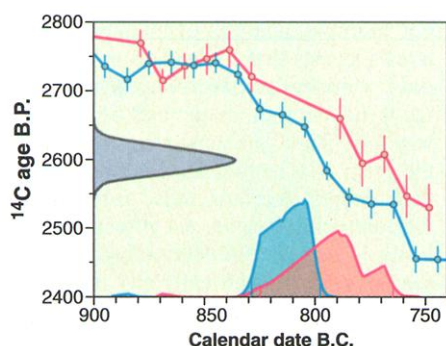
On page 2532 of this issue, Manning *et al.* (5) provide convincing evidence that a regional, time-varying ^{14}C offset can occur within a hemisphere. The authors attempted to match the radiocarbon ages of a “floating” tree-ring sequence (with unknown calendar age) from archaeological monuments in Anatolia (see the first figure) to the combined Northern Hemisphere data set (1). Only by excluding the ^{14}C measurements from the floating tree-ring sequence from ~750 to 800 B.C. could they find a good match. During this interval, the sequence shows a rapid increase in atmospheric ^{14}C that is not mirrored in the combined data set.

Now that the tree-ring chronology is “anchored” with an uncertainty of only a few years, the ring width pattern may be used to date

wood with well-preserved ring sequences from archaeological sites in the region. This independent scientific evidence may resolve several ongoing, and often intense, debates in Near Eastern and eastern Mediterranean archaeology. For example, using the new tree-ring chronology,

Manning *et al.* reevaluated the felling dates of timbers used in the construction of palaces at Achemhöyük and Kültepe IB. Together with seal imprints and documents of King Šamši-Adad I, these dates constrain the problematic Assyrian-Mesopotamian chronology to the more reliable Middle or

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The importance of regional radiocarbon offsets. Calibration of a hypothetical radiocarbon age of 2650 ± 20 ^{14}C years before the present (B.P.) (black) with the Northern Hemisphere calibration data set (blue data points) and the Anatolian tree-ring sequence (red data points). The 2σ calibrated age ranges (shaded areas) for the resulting probability distributions are 829 to 798 B.C. and 825 to 765 B.C., respectively. Calibration was done with CALIB 4.3 (17).

low-Middle Chronology (5). Manning *et al.* are also able to add support to the standard chronology of ancient Egypt from the dating of pieces of cargo wood from the Uluburun shipwreck, although this requires confirmation from timbers from the wreck itself. Furthermore, the 3 to 5 year growth anomaly found in the tree rings of the Anatolian sequence (~1650 B.C.), which may be a result of the volcanic eruption of Thera on Santorini, reinforces ice-core evidence for an older eruption date than previously indicated (6), with important implications for Aegean Bronze Age chronology.

On page 2529, Kromer *et al.* (7) further explore the magnitude and likely mechanisms of ^{14}C offsets. They report evidence that during a more recent interval of high ^{14}C production, radiocarbon ages for trees growing in Turkey are 17 years older than those of German trees with the same calendar age. The difference in the individual measurements is not statistically significant, but the trend in the data set is convincing. The authors conclude that the different growing season of the trees in the Mediterranean compared with those in Germany is responsible for the offset, which is seen only during a solar minimum when ^{14}C production is high.

To understand their reasoning, we must look at the mechanism of ^{14}C production. ^{14}C is primarily produced at high latitudes in the lower stratosphere by the collision of cosmic ray-produced neutrons with nitrogen. During periods of high solar activity, distortion of Earth's geomagnetic field by the solar wind prevents charged particles from entering the atmosphere and little ^{14}C is produced, whereas ^{14}C production peaks during periods of low solar activity

(solar minima). The atomic ^{14}C is quickly oxidized to $^{14}\text{CO}_2$ and enters the troposphere during the late spring, a period of high stratospheric-tropospheric exchange. By the next spring, the higher ^{14}C concentration in the atmosphere has been well mixed and diluted by exchange with other carbon reservoirs, particularly the surface ocean. The German trees, which grow mostly in the mid to late summer, take up more $^{14}\text{CO}_2$ during photosynthesis than do the Mediterranean trees, which grow in the spring and early summer.

Kromer *et al.* suggest that the colder and wetter climate associated with the solar minima may further accentuate the different growth patterns. The regional offset between the Turkish and German trees occurs during the early stages of the cooling associated with "Little Ice Age" glacial advances in Europe (8), and the Anatolian offset occurs during a well-documented cold period in the Northern Hemisphere (9, 10).

Regional radiocarbon offsets such as that between Germany and the Mediterranean will not have a noticeable effect on most radiocarbon calibrations, but they do make a difference to high-precision chronologies (see the second figure). It will be important to establish the maximum regional offsets for other regions and for other intervals of high ^{14}C production. Whether regional calibration data sets will become necessary or whether a correction

can be made in the calibration process will depend on how well we can understand and predict these offsets.

The confirmation of regional ^{14}C offsets has important implications, not only for high-precision chronologies in archaeological, geophysical, and paleoclimatic studies, but also for our understanding of variations in the exchange between Earth's carbon reservoirs. These offsets will be a challenge for climate modelers to explain.

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PERSPECTIVES: DEVELOPMENT

Staying a Boy Forever

Steven A. Wasserman and Stephen DiNardo

*I won't grow up.
I don't wanna wear a tie,
Or a serious expression
In the middle of July!*

—Peter Pan

Central to the homeostasis of many tissues and organs is a remarkable population of cells—the stem cells. These cells are endowed with two unique abilities: They can reproduce themselves (self-renew) and can produce pluripotent daughter cells that differentiate along different lineages to replenish tissues. Of paramount interest are the signals that

generate this stem cell Neverland, where mortality and maturation are both kept at bay. In particular, signals emanating from the microenvironment, or niche, where stem cells reside are believed to be important for determining stem cell fate. Studies of stem cell-dependent tissues—such as blood, skin, and sperm—have provided substantial insights into stem cell biology. A landmark achievement has been the propagation of pluripotent bone marrow stem cells (that differentiate into all types of blood cells) under defined culture conditions. But there are plenty of obstacles to studying stem cells, as they make up a vanishingly small fraction of the cell population within tissues. Difficult to unambiguously purify, they are usually only identified retrospectively, through complex serial culture assays that test their capacity for self-renewal and differentiation. Furthermore, many observations made on relatively heterogeneous stem cell popula-

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