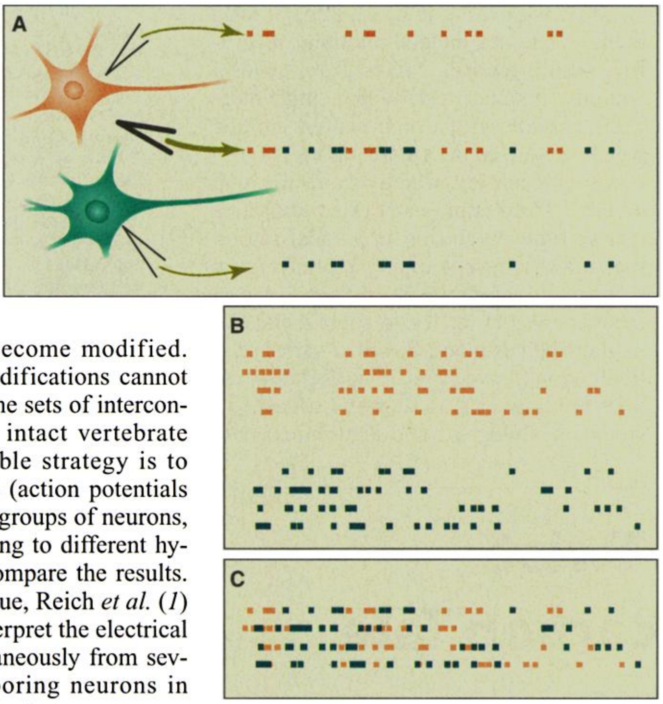
PERSPECTIVES: NEUROSCIENCE

Information Coding

Barry Richmond



When two trains collide. (A) Electrodes positioned near neurons record their electrical activity. Action potentials ~1 ms in duration are represented as electrical impulses over time (red and green blocks). Different electrodes record activity from different neurons, keeping the spikes separate (depicted as separate green and red streams of spikes coming from the thinner electrodes). Alternatively, one electrode might record the activity from several neurons (shown as a mixed stream of spikes coming from the thicker central electrode). Reich *et al.* compare separate spike data for two neurons with pooled spike data for the same two neurons. **(B)** Real impulses from two neurons after exposure of the subject to four stimulus presentations are shown as separate red and green impulse trains (each row depicts the relative times of the impulses following stimulus appearance). The set of impulses from the first neuron (red) has a tendency to have a gap in time just after an initial burst, whereas the set of impulses from the second neuron (green) has a steadier rate. The time gap represents one type of difference in the information carried by these two neurons. **(C)** Reich *et al.* compared the situation in (B) to one in which the impulse trains were pooled, as though they had been recorded from one electrode [the thick one in (A)]. All spikes were present, but the time relation among spikes arising from the same train was obscured. This made the gap in time less prominent, and therefore decreased the amount of different information available.

Information is encoded in the electrical signals generated by neurons in response to a stimulus. As these electrical signals flow along nerve axons and across synapses (points of contact between neurons) in the brain they, and hence the information they encode, become modified. Unfortunately, such modifications cannot be routinely studied in the sets of interconnected neurons of the intact vertebrate brain. The only available strategy is to record electrical signals (action potentials or "spikes") from small groups of neurons, to analyze them according to different hypotheses, and then to compare the results. On page 2566 of this issue, Reich *et al.* (*1*) examine how best to interpret the electrical signals recorded simultaneously from several individual neighboring neurons in monkey primary visual cortex.

They explicitly compare two codes, one in which they keep track of which neuron emitted each signal and the other in which the signals from a group of neurons are considered as a single pool (see the figure). The pooled-response code, which they show carries substantially less information, is particularly interesting because it is closely related to the averaging observed with techniques, such as functional imaging, that monitor activity across large numbers of neurons.

Despite the technical and data-analysis difficulties, the method of choice for studying local information modification and processing is to record the activity of single neurons under different experimental conditions. In their classic experiments recording electrical signals in the monkey primary visual cortex, Hubel and Wiesel (*2*) discovered that signal intensity (measured as the number of spikes) was related to the orientation of a bar of light (the relation between bar orientation and signal intensity is called orientation tuning). They also found that neurons encountered sequentially across the cerebral cortex had peak signals elicited by edges shifted in orientation by about 15° (*2*). However, both the number of spikes in the electrical signals and the time when they occurred varied substantially across seemingly identical presentations of a stimulus (see the figure, part B) (*3*, *4*). Because the tuning of nearby neurons is so similar when stimulated by oriented edges, averaging is potentially a good way to overcome response variability. Averaging is most effective when signals are correlated (that is, when signals elicited by the same stimulus rise and fall together) and when the differences between signals can be attributed to random differences in the noise. With a relatively large set of oriented bars, the signals from sets of individual neurons in primary visual cortex are considerably less correlated than with a smaller set of stimuli (*5*); the noise in primary visual cortex and other brain areas is somewhat correlated under these conditions (*6*–*8*).

When the information content of the signals of nearby neurons is measured using information theory—a statistical or signal-processing framework for describing the reliability of encoded information—neighboring neurons are found to carry only a small amount of redundant information (a result also reported here by Reich *et al.*). If most of the information were in the correlated part of the signals, we would expect a substantial degree of redundancy. Averaging spike counts across neurons underestimates the amount of information that is available. [Interpreting the relation between information, partially correlated signals, and noise has been discussed elsewhere (*9*)].

What about the importance of spike timing? Until 15 years ago, the patterns of spikes over time were generally ignored. It now appears, however, that variations in spike rate over time (*10*) (or perhaps specific times between action potentials) carry information that is not available from the spike count alone (although the precision with which spike timing should be represented is not settled, and may depend on the situation).

Reich *et al.* make simultaneous recordings from small sets of up to six single neurons located near each other in the monkey primary visual cortex. They explicitly ask whether or by how much information decreases when the spikes from these neurons are combined into a single train instead of keeping track of which neuron emitted each spike. For most sets of neurons, they find substantially more information when the code preserves the identity of the neurons emitting the spikes. This means that the relative timings across spikes emitted by a single neuron carry information that is only available by knowing which neuron

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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.

References

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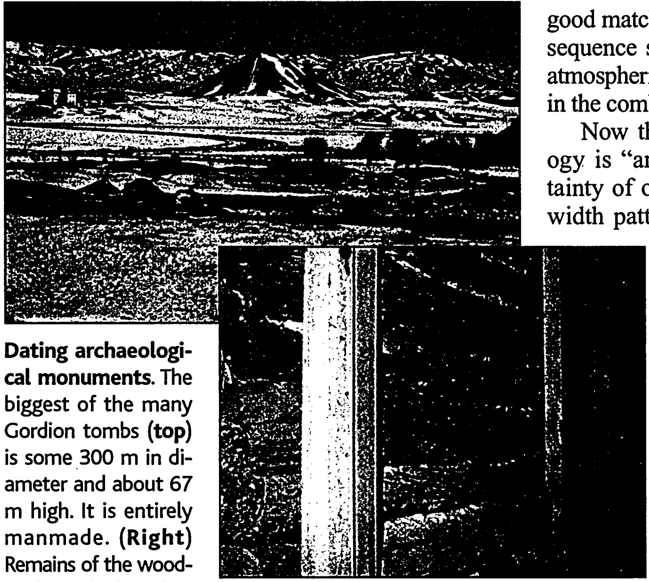
PERSPECTIVES: ARCHAEOLOGY

A New Twist in the Radiocarbon Tale

Paula J. Reimer

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 Acemhöyük 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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