excitatory inputs from the ICc to the ICx (*4*). These new neural connections respond to the excitatory neurotransmitter glutamate through synaptic membrane NMDA (*N*-methyl-D-aspartate) receptors (*5*).

New excitatory connections explain how neurons in the ICx respond to the appropriate position in space dictated by the altered visual map. But why do the ICx neurons stop responding to the old position? It turns out that the old excitatory inputs remain, but the ICx neurons now receive strong inhibitory input that is activated by the same auditory stimuli that activated the original excitatory connections. The inhibition sums with the excitation so that the ICx neurons no longer respond to the old stimuli. For the cells of the optic tectum that "listen" to the ICx neurons, the new auditory field appears similar in kind to the old one, but is just located in a different place. The neural circuitry that maintains the relocated receptive field is, however, quite different.

These findings explain why the normal auditory space map is restored in owls when the prism spectacles are removed, even at an age when normal owls have lost the ability to adapt to a rearranged visual map (*4*). The original neural circuitry is still there, and all that is needed for it to assume control is removal of inhibitory input. Inhibitory connections also explain why the capacity for plasticity in adult owls is greater if they have adapted to rearranged maps as juveniles (*6*).

What rule of neural plasticity regulates the strength of these inhibitory connections? Inhibition is selectively increased for those positions in space that receive strong excitatory input but do not match the position at which ICx neurons target cells in the optic tectum. Such a rule requires that a retrograde signal travels from the tectal cells to the axonal terminals of the ICx cells and thence to their cell bodies and dendrites, where it enhances responses to inhibitory inputs at GABA receptors. These dual contingencies show that inhibitory connections are weakened under circumstances in which excitatory connections are strengthened and vice versa (*7*). Such a reciprocal relationship between the excitatory and inhibitory inputs makes sense, although as yet has not been rigorously demonstrated.

How applicable are the new findings to the plasticity of other types of sensory maps? There is little evidence for selective inhibition as the mechanism of plasticity in the adult cortex—most long-range connections are excitatory not inhibitory. However, a combination of excitatory and inhibitory pathways may explain cases in which receptive fields move, for example, after denervation of a digit or of two adjacent digits (*8*). In contrast, experiments in the visual cortex show that the loss of response to the occluded eye after brief monocular deprivation is not the consequence of selective inhibition from deprived-eye pathways (*9*). Nonetheless, appropriate inhibition is essential for normal plasticity in the visual cortex (*10*).

In the brain, as in life, it is not just what you do that matters, it's also what you don't do. The plasticity of auditory spatial representation in the owl brain depends not only on new excitatory connections but also on overwhelming the persistent old connections through inhibition. By combining and overlaying different plasticity mechanisms in the auditory pathway, the owl is able to adjust its various sensory maps so that they are in harmony.

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PERSPECTIVES: CLIMATE WARMING

Seeing the Wood from the Trees

Keith R. Briffa and Timothy J. Osborn

In recent years, several studies (*1–5*) have attempted to reconstruct the history of hemispheric or global average surface air temperatures for much, or all, of the current millennium. The motivation for these studies is our need to establish the degree to which the 20th century is unusually warm when viewed against a background of preindustrial climate variability. Some papers describe simple averages of selected long temperature proxies (indirect recorders of temperature conditions), mostly annually resolved time series derived from tree rings, ice cores, and some corals. Others also incorporate the longest instrumental series stretching back into the 17th and 18th centuries. This direct averaging approach gives equal weight to each series and relies on sufficient regional coverage to provide a true representation of hemispheric or global conditions.

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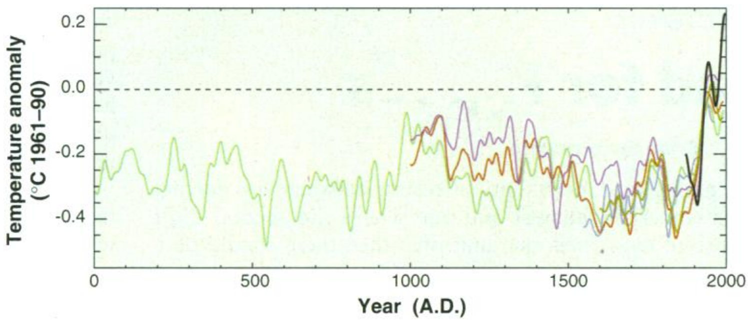
The alternative approach is multiple regression, where greater weight is placed on specific proxy series that exhibit greatest affinity with the modern large-scale instrumental record (*5*). The latest such study by Mann *et al.* (*6*) extends their previous reconstruction of Northern Hemisphere (NH) mean annual temperatures from A.D. 1400 back a further 400 years. This is important because much of the period from 1300 to the start of widespread instrumental records may have been relatively cool, thus potentially exaggerating the long-term significance of the observed 20th century warming. It has long been suggested, mostly on the basis of European information, that the medieval period may have been relatively warm, but the evidence from further afield is equivocal. A reliable, early NH temperature reconstruction is, therefore, a more appropriate benchmark against which to gauge the significance of 20th century warmth. In attempting to provide this, Mann *et al.* confront a number of problems currently limiting our ability to view such reconstructions as realistic indications of the full amplitude of past temperature changes.

An uninformed reader would be forgiven for interpreting the similarity between the 1000-year temperature curve of Mann *et al.* and a variety of others also representing either temperature change over the NH as a whole or a large part of it (see the figure) as strong corroboration of their general validity, and, to some extent, this may well be so. Unfortunately, very few of the series are truly independent: There is a degree of common input to virtually every one, because there are still only a small number of long, well-dated, high-resolution proxy records.

Mann *et al.* base their early (pre-1400) reconstruction on 12 series, of which nine are derived from tree rings and three from ice cores. Commendably, they present two standard error confidence limits on this reconstruction and show how these are considerably wider before 1600 than in later centuries. The upper bounds of the early limits are high enough to encompass even the upper limit of uncertainty associated with their 20th century temperature estimates (which run up to 1980). The warmth shown in the instrumental records during the past two decades, however, is clearly greater than the upper boundary of uncertainty for the warm medieval period.



Records of past climate... Comparison of NH temperature reconstructions, all recalibrated with linear regression against the 1881–1960 mean April–September instrumental temperatures averaged over land areas north of 20°N. All series have been smoothed with a 50-year Gaussian-weighted filter and are anomalies from the 1961–90 mean. Instrumental temperatures (1871–1997) are in black, circum-Arctic temperature proxies [1600–1990, from (*2*)] are in yellow, northern NH tree-ring densities [1550–1960, from (*3*), processed to retain low-frequency signals] are in pale blue, NH temperature proxies [1000–1992, from (*4*)] are in red, global climate proxies [1000–1980, from (*5, 6*)] are in purple, and an average of three northern Eurasian tree-ring width chronologies [1–1993, from (*10*)] is in green. Although representing a much more restricted spatial coverage than the other series, the last of these (also processed to maintain low-frequency climate information) is included here because of its extended length and because it suggests relatively cooler summer temperatures (at least across northern Eurasia) before A.D. 1000.

The confidence levels around the Mann *et al.* NH series are based on calibration against the instrumental record. However, additional uncertainty may come from the earlier sections of the tree-ring data, because tree-ring chronologies often exhibit a progressive degradation in statistical quality further back in time, a product of their diminishing internal replication (that is, series are often made up of fewer samples). Also, the production of a long tree-ring chronology normally involves some degree of detrending (known as "standardization") to reduce bias in the final chronology resulting from temporal changes in the average age of the samples (young trees have wider and more dense rings than older ones). As a result of standardization, many long tree-ring chronologies may not represent all of the long-term climate variability that influenced tree growth in their region.

Mann *et al.* state that one particular candidate predictor in their regression, the amplitude series relating to the first principal component of a group of high-elevation tree-ring chronologies in the western United States, is essential before A.D. 1400 for a verifiable NH reconstruction. Unfortunately, these trees display a progressive increase in growth from the middle of the 19th century, which may be wholly or partly due to rising atmospheric CO_2 levels. How can we distinguish the growth-promoting effects of warm temperatures from the possible influence of increasing CO_2 and perhaps even other anthropogenic growth enhancers such as nitrogenous pollution? All show positive trends over the 20th century, and each has the potential to increase tree growth alone or in combination with others (regardless of whether that growth is limited by moisture availability or temperature).

Mann *et al.* adjust the time series of these crucial high-elevation U.S. trees by comparing it with a separate record of growth at the northern North American tree line and assuming that the trend in the residuals is nonclimatic. They state that "there is no a priori reason to expect the CO_2 effect ... to apply to the northern tree line series" (*6*, p. 760). However, there is accumulating evidence of enhanced growth of trees in many NH regions during the 19th and 20th centuries. This is unlikely to be a simple linear response to greater warmth alone (*3*, *7*). It may often not be easy to recognize this enhancement because of the standardization of tree-ring chronologies and because it may be masked by the normal (age-related) declining growth trends in many tree-ring time series.

CORRELATIONS WITH TEMPERATURE*			CROSS CORRELATIONS†			
Proxy series	Apr.–Sep.	Decadally smoothed	(*4*)	(*5, 6*)	(*3*)	(*10*)
(*4*)	0.71	0.85	–	0.71	0.78	0.78
(*5, 6*)	0.76	0.92	0.46	–	0.62	0.60
(*3*)	0.65	0.83	0.54	0.37	–	0.83
(*10*)	0.60	0.82	0.48	0.40	0.47	–

*1881–1960. †Cross correlations between proxies over maximum overlap period (yearly values below diagonal; after 50-year smoothing above diagonal).

The temperature histories that extend through the medieval period do indicate general warmth (see the figure), although with different maxima (in the 9th, 10th, and 11th centuries). Clearly none of these reach the levels of warmth seen today [although the confidence ranges (not shown here) approach them]. On the basis of their analysis, Mann *et al.* conclude that the 20th century is anomalously warm. Even with the very limited data available and the problems associated with interpreting many of them as unambiguous measures of hemispheric temperature change, this conclusion must surely be accepted. However, many more data and much work are necessary before we can reduce the large uncertainties associated with reconstructions of medieval and earlier temperatures on large spatial scales. Long data sets from many, and more diverse, areas of the world are essential if we are to achieve a more accurate hemispheric overview and acquire a useful picture of the influences of important regional climate phenomena such as the history of the El Niño–Southern Oscillation or North Atlantic Oscillation (*8*). Not least, we need up-to-date studies of the responses of trees, and other high-resolution proxies, to the dramatic increases in hemispheric and global temperatures measured in the past two decades and their interactions with the other environmental changes that are occurring simultaneously. A number of tree-ring chronologies have displayed anomalous growth or changed responses to climate forcing on different time scales in very recent decades (*3*, *9*). Understanding the reasons for these changes is important for understanding the causes and limits on past tree growth. Paradoxically, therefore, more work in the recent period is required to better interpret the early proxies. Few of the proxy series run up to the present, however, and updating these will involve considerable effort.

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