PERSPECTIVES: NEUROSCIENCE

Memories Are Made of This

Michael D. Rugg

Why can we recollect some events but not others? Part of the answer is that all events are not equal; they differ in how they are initially encoded into memory. Memory encoding—the term for processes that mediate between the experience of an event and the formation of a memory of that experience—is affected by many factors (*1*). Two in particular stand out: An event is most likely to be remembered if it is given undivided, not partial, attention, and if this attention is directed to its meaning rather than to more superficial attributes (such as physical appearance).

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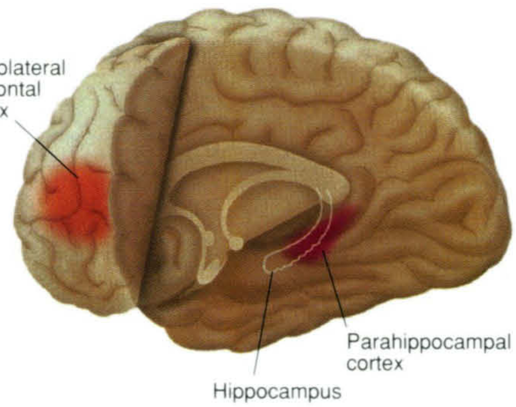
Although certain brain regions (notably, the hippocampus and adjacent regions in the medial temporal lobe) are known through lesion studies to be required for formation of durable memories (*2*), it has proven difficult to determine which regions specifically underlie the process of memory encoding. The advent during the past decade of functional neuroimaging, and with it the means to image the brain activity of normal individuals during encoding, allow this question to be tackled from a new angle. Two reports in this issue by Brewer *et al.* (page 1185) and Wagner *et al.* (page 1188) (*3*) showing that neural activity in certain brain regions predicts subsequent memory performance mark a significant step forward.

The authors of both studies took advantage of recent developments in functional magnetic resonance imaging (fMRI). They obtained measures of the neural activity (as indexed by blood oxygenation level) elicited by single items as they were presented to individuals performing an "incidental" encoding task (in which the instructions make no reference to the need to memorize the material). The items (pictures in Brewer *et al.*, words in Wagner *et al.*) were later classified as to whether, in a subsequent recognition memory test, they were remembered well, remembered only weakly, or were forgotten. In two brain areas—the prefrontal and parahippocampal cortices—neural activity elicited by items that were well remembered was greater than the activity elicited by weakly remembered or forgotten items (see the figure). These findings echo those from earlier studies in which event-related potentials (ERPs) were used to look for event-related brain activity predictive of subsequent memory (*4*). Unlike ERPs, however, the activity detected by fMRI can be localized with great precision.

The prefrontal cortex has already been identified by neuroimaging studies as a region likely to participate in memory encoding. Several regions of the left prefrontal cortex show higher activity as the amount and complexity of semantic processing rise; such findings have been taken as evidence that the left prefrontal cortex underpins the beneficial effects of semantic processing on subsequent memory (*5*). The findings from Wagner *et al.* provide striking support for this proposal.



Encoding hot spots. The prefrontal cortex and the parahippocampal cortex of the brain are active during the encoding of memories.

ILLUSTRATION: K. SUTLIFF

Several of the areas in which these authors found neural activity to predict subsequent memory performance were located in the left prefrontal cortex. In a separate experiment, Wagner *et al.* found that these areas also showed enhanced activity when words were categorized on the basis of semantic rather than physical attributes. Thus, for words at least, the left prefrontal cortex supports cognitive operations that contribute to effective memory encoding, and these operations include analysis of the meaning of the item. Because the functional images obtained by Brewer *et al.* excluded most of the frontal lobes, it is not possible to tell whether their finding of encoding-related activity in right posterior prefrontal cortex indicates that this region was engaged instead of, or in addition to, more anterior prefrontal regions on the left.

Both studies also found that activity in the parahippocampal cortex also predicted later memory performance. This activity was bilateral in Brewer *et al.*, but confined to the left hemisphere in Wagner *et al.*, a difference that presumably reflects the differential lateralization of memory for pictures and words. Earlier neuroimaging studies provided indirect evidence of a role for the parahippocampal cortex in encoding: Activity in this region is greater for items that are novel than for familiar items (*6*). Because their experimental items were all equally novel, the findings of Brewer *et al.* and Wagner *et al.* indicate that this region does more than participate in novelty detection. The parahippocampal cortex may respond to items that are made "memorable" by a variety of different kinds of processing—elaborate semantic analysis, for example, or attentionally demanding processing triggered by an item's novelty.

There was no evidence in either study of neural activity predictive of subsequent memory in the hippocampus proper. Because this structure is thought to be a key component in the neural circuitry supporting conscious memory, these negative findings may seem surprising. In fact, little can be concluded from them. Although they could signify that the hippocampus plays a more limited role in memory encoding than might have been supposed, these results could just as well indicate that the neural correlates of encoding in the hippocampus are not always associated with a change in net metabolic demand on a spatial scale detectable by fMRI (~2 to 3 mm).

This issue notwithstanding, the findings of Brewer *et al.* and Wagner *et al.* demonstrate that the functional neuroimaging of human memory has entered an exciting new phase, in which localized neural activity elicited by a single event can potentially be linked to a whole range of different memory measures. It is important, however, not to lose sight of the fact that functional neuroimaging is only one of several methods that are needed to achieve an understanding of the cognitive neuroscience of memory. For example, an important question raised by the findings discussed above concerns the nature of the relation between the prefrontal and parahippocampal cortex during encoding. Do these regions operate serially to support effective memory encoding, as suggested by Wagner *et al.*, or do they act

The author is in the Wellcome Brain Research Group, School of Psychology, University of St. Andrews, St Andrews KY16 9JU, UK. E-mail: mdr@st-andrews.ac.uk

independently, perhaps by providing separate inputs to a common structure such as the hippocampus? The fMRI method cannot fully address this question. Lesion studies are required to determine which of these regions is actually necessary for new memories to be formed. And electrophysiological studies, with electrical or magnetic measures, are needed to achieve the temporal resolution necessary to determine if these regions are activated serially or concurrently. In short, the full benefits of functional neuroimaging data are gained when these are used to inspire and inform studies using other methodologies.

References and Notes

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PERSPECTIVES: CLIMATE CHANGE

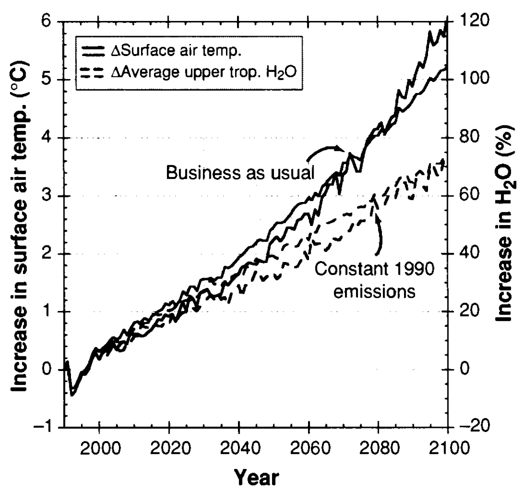
Just Add Water Vapor

David Rind

For those who believe that global warming will not be an issue in the next century, the behavior of water in the atmosphere is crucial. Global climate models show that increased warming will lead to greater evaporation from the ocean; with doubled carbon dioxide and more water vapor (an excellent greenhouse gas), the warming would be substantially more than 2°C. Add to this the expected retreat of sea ice and snow cover, which allows more sunlight to be absorbed, and the warming reaches 3°C (more than half of the change since the last ice age). Yes, clouds may act to mitigate things, but they may also amplify the warming, as is the case in many climate models. Aerosols, such as sulfates released during fossil fuel burning, may slow the warming by reflecting sunlight away from Earth, but because they are somewhat easier to limit than CO_2, we will probably clean up the air for health reasons and so exacerbate the warming.

As the lower tropospheric water vapor concentration would likely increase along with surface air temperatures, recent attention has focused on the upper troposphere, which is equally as important in terms of radiative transfer. Lindzen suggested that with increased convection and more vertical motion in the tropics, there would be increased subsidence bringing dry air down from higher levels and decreased moisture above about 6 km (*1*). Note how this deviates from model predictions (see figure, where upper tropospheric water vapor increases about 20% per degree Celsius of surface warming).

I, as well as many others in this field, believe that future reductions in high-altitude moisture are very unlikely; they would have to co-exist with low-altitude increases in an atmosphere that has many ways to mix moisture vertically. Furthermore, unless the current climate just happens to have the maximum moisture aloft, the theory also implies that colder climates should be wetter at high altitudes; with less evaporation and convection, where would the moisture come from, and how would it get up there? Such arguments aside, it would nice to be able to test either expectation or, perhaps more importantly, to determine whether climate models produce the proper magnitude of the water vapor feedback. Unfortunately, we do not have the observations in place to be able to do so, and it is not clear when we will.



Wetter weather. Surface air temperature and percentage change in specific humidity in the upper troposphere (trop.) from the GISS model for two scenarios of trace gas emissions: business as usual (solid lines) and the (climatically ineffective) constant 1990 emissions (dashed lines). No aerosol increases are used, and, given the relatively high model sensitivity (1°C W^{-1} m^{-2}), this represents almost a worst case scenario. For reduced warming, the change in upper tropospheric humidity would be proportionately less, and thus the accuracy needed to observe it would need to be that much greater.

Historically, water vapor values above the surface have been measured by sensors on radiosondes. As is well known, these cannot be used to assess trends: They are geographically restricted, being found mostly over land in the Northern Hemisphere, and worse still, different sensors give different absolute water vapor values. Poorer instruments respond too slowly and overestimate water vapor amounts at high levels. As these deficiencies become known, and countries (including the United States) shift to better sensors, it may well appear that the upper troposphere is drying simply because of the better instrumentation (*2*).

Satellites, with global data collection, ideally could provide an answer for the recent past except that they have their own problems. Downward-looking instruments cannot see with good vertical resolution; results are generated for 300-mbar-thick layers (that is, layers defined on a pressure scale), which are too coarse to properly calculate radiative forcing changes. Limb-scanning instruments have large horizontal footprints, which are tricky to interpret for a constituent so heterogeneous in space and time. Furthermore, they were designed for stratospheric monitoring and tend to have large error bars for data collection in the upper troposphere. Clouds also present problems, lowering the accuracy even for microwave instruments. New sensors becoming available as part of NASA's EOS research program, as well as for European and Japanese missions (and ultimately to be used on operational satellites), will have better radiometers, but it is yet to be proven that they can overcome these difficulties. And, with cutbacks in the EOS program by the U.S. Congress and a certain disinterest on NASA's part in acting as a monitoring agency, current plans do not envision most of them remaining aloft long enough for trends to be determined anyway.

Stratospheric water vapor increases could also amplify the greenhouse effect and, with less variability and cloud cover interference, should be easier to measure (doubled stratospheric water vapor provides radiative forcing of about 1/7 that of doubled atmospheric CO_2). There are indications that it might already be increasing (*3*). Unfortunately, here too measurement

The author is at NASA/Goddard Institute for Space Studies, New York, NY 10025, USA. E-mail: drind@giss.nasa.gov