Remembering Outside the Box

Article *in* Science · August 2009

DOI: 10.1126/science.1177156 · Source: PubMed

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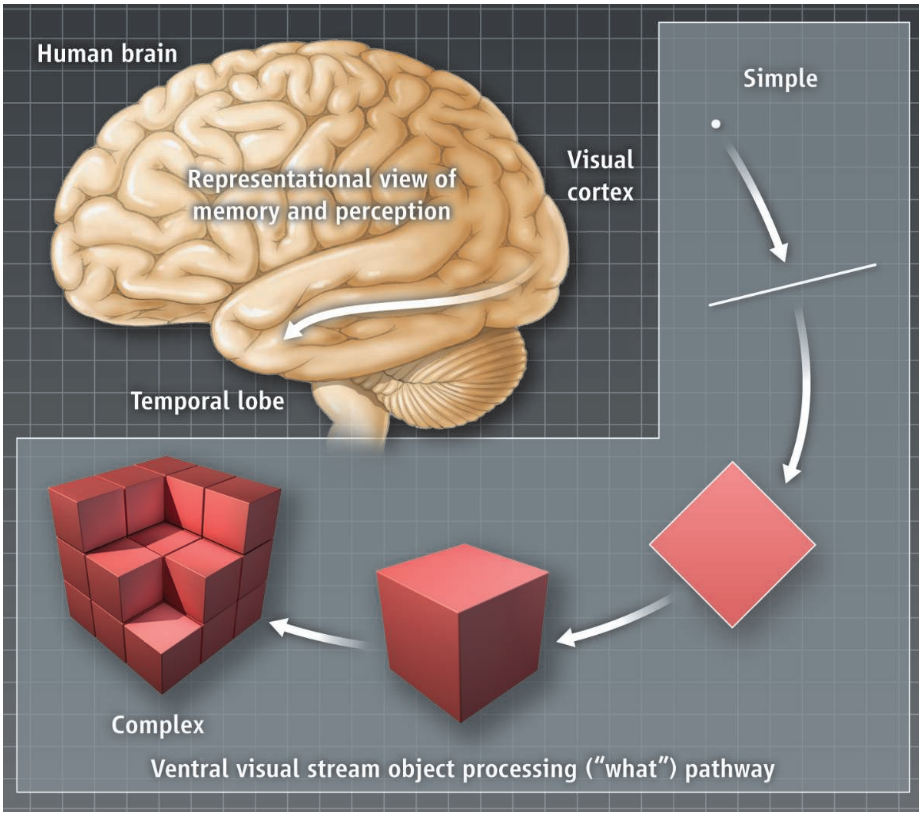
NEUROSCIENCE

Remembering Outside the Box

The mammalian brain may be organized in terms of multipurpose representations rather than psychologically defined modules.

Lisa M. Saksida



Brain organization. The standard view in memory research suggests that distinct brain regions support different cognitive functions. The representational view of the human brain, by contrast, suggests that a given brain region could be useful for multiple high-level functions. For example, information represented in the "what" pathway flowing through the visual cortex to the medial temporal lobe may be important for both memory and perception.

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The prevailing view in memory research is that the mammalian brain is composed of a number of heterogeneous modules, each responsible for a different cognitive function, including different types of memory. An emerging alternative view, however, suggests that instead of such modules, the brain is organized in terms of the multipurpose representations that different regions support. As such, a given representation—and thus a given brain region—could be useful for many different functions. Evidence for this latter view has focused largely on demonstrating that regions within the putative memory system of the mammalian brain also play a role in another high-level function: perception (*1*–*4*). On page 87 of this issue, López-Aranda *et al*. (*5*) show that regions within the brain's putative perceptual system also play a role in memory, further solidifying evidence for a representational view of brain organization.

The dominant textbook paradigm of human memory is the multiple memory systems view, according to which different kinds of memory, such as declarative memory (memory for facts and events) and nondeclarative memory (memory for skills and procedures), are subserved by different modules in the brain (*6*, *7*). Declarative memory is the domain of the medial temporal lobe memory system, which includes structures such as the hippocampus and perirhinal cortex. This system can be contrasted with a separate perceptual representation system (*8*), which includes the extrastriate visual cortex (comprising roughly 30 regions including, V2, V3, V4, and IT in the primate brain). This perceptual system is, according to the standard view, critical both for representing the structure of visual stimuli and for nondeclarative memory functions such as priming (an increase in sensitivity to a stimulus due to prior experience).

However, it may be more useful to think about brain regions, not in terms of psychologically defined modules, but in terms of the representations that they contain (*9*–*12*) (see the figure). For example, in visual memory, structures within the medial temporal lobe (such as the perirhinal cortex) may be understood as an extension of the ventral visual object processing system—or the "what" pathway—which flows from the visual cortex to the medial temporal lobe (*13*, *14*). This view suggests that structures in the "what" pathway and the medial temporal lobe should not be segregated according to their putative roles in perceptual versus mnemonic function. Instead, the entire stream is important for multiple functions including both memory and perception.

A behavioral paradigm that has been critical in establishing the multiple memory systems view is object recognition memory. In this model, a subject is presented with an object to study. After a delay, the study object and a novel object are presented. A typical subject will preferentially select or spend more time investigating the novel object, and this is taken to be an index of memory for the study object. Object recognition memory is considered to be a canonical example of declarative memory and is therefore thought to depend exclusively on the medial temporal lobe memory system (*15*). However, López-Aranda *et al*. demonstrate the involvement of an area outside this system—specifically, cells that comprise layer 6 of the extrastriate visual cortical area V2. In their study, lesions of cells in layer 6 of the V2 region in the rat brain impaired object recognition memory, which suggests that V2 is critical to this function. This is not consistent with the prevailing multiple memory systems view, which would predict that damage to regions outside the medial temporal lobe should have little effect on object recognition memory. This finding is consistent, however, with the representa-

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tional view, which would predict that damage to any region within the ventral visual cortex–to–hippocampal stream could affect object recognition memory.

It might be argued that damage to the V2 region may have cut off visual information to the medial temporal lobe. Such a disruption would render the medial temporal lobe memory system unable to function properly, thereby making the findings of López-Aranda *et al.* consistent with the modular view of memory. However, lesions made in the V2 region were highly selective in that an excitotoxin was used to damage only cell bodies in V2. Thus, neuronal extensions (fibers) would have been left intact, passing from V1 through V2, to downstream areas. Thus, visual information could still pass through V2. There were also plenty of "jumping projections" from neurons in information processing regions upstream of V2 to regions downstream from V2, including the medial temporal lobe.

More interestingly, López-Aranda *et al.* have provided further evidence to suggest that the involvement of V2 in object recognition memory cannot be interpreted simply in terms of a lack of information flowing from the visual cortex to the medial temporal lobe (due to V2 cell damage). When the protein RGS-14, which is involved in signaling pathways implicated in memory, was overexpressed in cells of layer 6 in V2, rats could remember more objects, and for much longer, relative to controls. The same manipulation within the medial temporal lobe (specifically, within the dentate gyrus and CA1 region of the hippocampus) had no effect on object recognition memory. Thus, López-Aranda *et al.* show that manipulations outside of the putative medial temporal lobe memory system can both impair and facilitate object recognition memory. This result is also consistent with previous studies reporting no effect of hippocampal manipulations on object recognition memory and is consistent with the view that the medial temporal lobe memory system is not a homogeneous system but contains distinct, dissociable components (*16*, *17*).

An outstanding question is how molecules such as RGS-14 facilitate memory and what function they have in the mechanisms of cognition in the normally functioning brain. These are critical questions for future research.

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10.1126/science.1177156

ECOLOGY

Insect Conservation

Understanding of ecosystem interactions and management has led to a major advance in the conservation of specialized insects.

Josef Settele and Elisabeth Kühn

Conservation efforts in Europe mainly aim to preserve and manage ecosystems that contain putatively endangered biotic communities. However, as Thomas *et al.* show on page 80 of this issue (*1*), this approach may not yield the desired results—particularly in the case of comparatively specialized taxa such as butterflies and other insect groups.

Many insects react rapidly to environmental change. For example, regional extinction rates of European butterflies have exceeded those of birds and higher plants by an order of magnitude in recent decades (*2*). Ensembles of closely interacting species are most vulnerable to change, because survival depends on the persistence of multiple group members. Thus, the greatest declines among butterflies were recorded in the many species that also depend on ants (myrmecophiles) (*3*). The best-documented example is the decline in the second half of the last century and eventual extinction in the UK in 1979 of the Large Blue *Maculinea arion* (*1*), a butterfly that during the first three larval stages depends on specific food plants (*Origanum* or *Thymus*) and later on the brood of specific *Myrmica* ants.

To improve the prospects for at least some insect groups, the 1992 European Habitats Directive listed examples of myrmecophiles (*4*), including three of the five European *Maculinea* species. All listed species must be kept in a favorable conservation status through appropriate management in the European-wide network of conservation areas called Natura 2000. However, because little was known about the biology of these species, conservation success was limited—and still would be, had it not been for groundbreaking research on *Maculinea* ecology started in the UK by Jeremy A. Thomas in the 1970s and joined from 1983 onward by Graham Elmes. Particularly in the 1990s through research by several labs, *Maculinea* became a key taxon in evolutionary and conservation biology.

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Conservation under climate change. Through landscape management, it may be possible to mitigate climate change effects on species such as the Large Blue *M. arion* (**top**) and the Dusky Large Blue *M. nausithous* (**bottom**).