The memory storehouse

The quite interesting debate on *Visual imagery and visual representation*, in the July issue of *TINS*, 1994, will surely have provoked numerous *Gedankenexperimente* on encoding and decoding processes of the brain. In their Fig. 1, Sakai and Miyashita[1] referred to the likely existence of a 'memory storehouse' that (for visual information) would be situated in the temporal association cortex, and would be controlled by 'memory controllers' (structures of the medial temporal lobe, including the hippocampus).

While 'formalizing' memory circuits has tradition[2] and might lead to greater understanding, it can, on the other hand, undermine these circuits. In my opinion, however, neuroscientists not so familiar with the current status of the memory discussion[3] might be driven by Sakai and Miyashita's article to take it for granted that there are circumscribed memory storehouses in human brain. I question this view largely on the basis of neuropsychological data.

It is known that memory is strongly time-related and that the figure of a Janus head best symbolizes the retrograde and anterograde sites of memory, namely that, as a result of focal brain damage, patients might be unable to acquire new information[4,5] while still having (largely) retained their pre-morbid level of episodic memory knowledge, or that they might suffer an inability to decode old memories in the presence of a preserved recent memory ability[6,7]. Therefore, evidence from single cases with selective anterograde or retrograde amnesia suggests that we have a number of bottleneck structures necessary for successful information encoding (for example, medial diencephalic structures[3,5]), and that there are other structures necessary for information decoding. Consequently, there is a certain independence between these two Janus head-like time sides.

Mnemonic information processing is most likely a matter of the whole brain with some structures being more centrally engaged than others. There is a critical difference between what a given brain can do without a particular region and what this particular region contributes to[8], or in other words, while some functions (including memory) might be grossly impaired after focal brain damage this does not suggest that only this region is critical for those functions. The network character of information processing has been emphasized throughout the past two decades[9,10], and is supported by the numerous connections between individual neurons both on the afferent and on the efferent side. Therefore, it is short-sighted to assume the existence of anatomically narrow defined storehouses for memory. Engrams are more likely represented in widespread nets, and it is also most likely that different brain structures work as memory controllers for the encoding and the decoding site.

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Reply

In his letter, Markowitsch questions the idea of memory storehouses on the basis of human lesion studies. In those studies, it is indeed difficult to relate focal brain damage to a particular type of memory impairment. However, it should be noted that the results of animal lesion studies and neurophysiological studies have provided complementary data. In this reply, we show that the idea of memory storehouses is based on current understanding in the neurosciences, and that it is compatible with neuropsychological data.

In our model of the cognitive memory system (Fig. 1 of Ref. 1), we specified that it is based on visual-object memory. It has been proposed that the temporal association area, or the inferotemporal (IT) cortex, is a possible candidate for the memory storehouse in the visual memory system for object recognition[2–4]. This idea, however, does not mean that IT cortex is the general memory storehouse for all possible types of memories. It is simplistic and misleading to refer to general 'mnemonic information processing' as if it were 'a matter of the whole brain', as Markowitsch stated. Modality-specific visual memory is localized in the sense that it is stored within a part of the cortical visual areas[5] but not in the motor or other cortices. In the long history of searching for engrams (for review, see Ref. 6), it has been shown that the visual memory system can be further subdivided. Mishkin and his collaborators demonstrated that monkeys with anterior IT lesions are impaired markedly in the object-recognition memory task, but not in the visuospatial memory task[3,7]. This behavioral evidence has been supported by our recent findings of neuronal correlates of visual memory storage and retrieval in the anterior IT cortex[8]. Visual object memory is distributed in the sense that it is represented in multiple IT neurons[4].

In favor of the cortical localization of the storehouse, Mishkin[3] commented that 'the older memories were stored upstream from both the limbic system and the medial thalamus, presumably within the cortical areas', because global amnesia following either medial temporal or medial thalamic injury is mainly anterograde in nature. The anterior IT cortex is

well suited for memory storage of objects because it is the final stage of the occipital–temporal pathway specialized for the analysis of form and color[5,9]. More direct evidence is the retrograde amnesia of events and visual material, which follows focal pathology in bilateral anterior temporal lobes[10,11]. This observation is actually consistent with the conclusion of a case report by Markowitsch and colleagues[12] that 'the necessary anatomical substrate for the retrieval of old episodic memories lies *within* the anterior temporal regions' (emphasis not in original). By combining approaches of neuroimaging and neuronal recording with lesion analysis, the memory storehouse could be further characterized.

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Beyond 'pet' methodologies to converging evidence

Roland and Gulyás[1] recently sparked debate in this journal by asserting that the neural representations underlying visual mental imagery are nonretinotopically organized. They based their case primarily on the results of their own research with positron emission tomography (PET). Although some commentators drew upon evidence from other techniques, no-one pointed out the substantial body of results, obtained using a variety of methods other than the currently popular PET and functional nuclear magnetic resonance imaging (MRI), that contradicts Roland and Gulyás' hypothesis.

Overlooked evidence

In addition to the PET and functional MRI evidence that was the focus of the debate[1], there is relevant evidence from single-photon emission computed tomography (SPECT), as well as from scalp-recorded brain potentials, studies of brain-damaged subjects, single-unit recordings in monkeys, and even psychophysical studies in normal subjects. Because of the length limitation for letters, this evidence can be only summarized briefly here.

Goldenberg and colleagues[2–6] have used SPECT to examine a wide variety of mental imagery tasks, along with control tasks that tap similar processes except for the imagery itself. In six of nine experiments, imagery was associated with occipital activation and, in the seventh, subjects' reports of image vividness correlated with occipital activation. Charlot *et al.*[7] also find occipital activation with SPECT.

Turning to EEG, visual mental imagery has long been associated with occipital alpha-wave suppression[8], even relative to tactile mental imagery[9]. The generation of visual images from memory, cued visually or auditorily, causes a positive deflection of the event-related potential (ERP) maximum over the occipital scalp[10]. DC shifts associated with imagery also show occipital maxima[11]. Images modulate the visual ERP as a function of the match in shape between the image and stimulus, and this modulation is also maximum over occipital scalp[12].

Acquired achromatopsia is often accompanied by the inability to visualize objects in color[8]. As color vision is presumably a function of retinotopically organized areas, this implies that at least some of these areas are used for visual imagery. A more direct demonstration of the importance of retinotopically mapped occipital cortex in mental imagery comes from our study of a patient who underwent unilateral occipital lobectomy[13]. When the maximum size of her visual mental images was measured before surgery, it was normal. After surgery, it was reduced by approximately half, and along the horizontal axis only, consistent with a role for retinotopically mapped visual cortex in mental imagery.

Haenny and colleagues[14] trained monkeys to anticipate a visually displayed target line of a particular orientation by means of a tactile cue, and found that upon presentation of the cue, activity could be recorded in some of the same neurons in area V4 that are activated by the sight of the line. Although it is impossible to say whether the monkeys in this experiment experienced mental images, they did generate endogenous activity in retinotopically organized visual cortex.

In psychophysical studies with normal subjects, imagery selectively affects perception only when image and percept are perfectly superimposed; a half-degree shift eliminates the effect[15], implicating a spatially mapped representation. By interposing eye movements between image formation and stimulus presentation, a specifically retinotopic representation has been demonstrated[16]. Finally, as previous commentators pointed out, some PET and functional MRI studies also find occipital activity during imagery[17].

Is it still possible that imagery does not include retinotopically organized visual representations?