

# The Cortical Distribution of Sensory Memories

## Minireview

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This review considers evolving concepts about how different functional regions of the cerebral cortex contribute to the storage and retrieval of sensory information. Two hypotheses appear consistently in the cognitive neuroscience literature on this topic: first, that sensory information is stored within distributed networks that span cortical territories; second, that sensory information processing is organized hierarchically, proceeding sequentially from “early” cortical areas (devoted to extraction of elemental features from sensory input) to “late” cortical areas (where elaborated and integrated representations of sensory information are constructed). Most studies have emphasized the storage of sensory information in the hippocampal complex (see Horel, 1994, for discussion) or in “association” cortical areas, such as inferior temporal, posterior parietal, and prefrontal cortex—areas where neurons respond best to complex sensory stimuli (e.g., faces or objects), often from multiple sensory modalities, and are located several synapses downstream from the principal sensory input to cortex (e.g., Mesulam, 1998). Consistent with this view, recent work has uncovered the interplay between frontal and temporal cortical regions during memory storage and retrieval. What role, then, remains for “early” sensory cortical areas? It is common to relegate them to the role of on-line processing of sensory information: that is, stimulus-related information is present while a sensory stimulus is present, but quickly vanishes at termination of the stimulus itself, to be reestablished only at arrival of the next afferent signal. But recent observations point toward a new conception in which sensory cortex also has an essential role in the *storage* and *retrieval* of certain types of memories. Here we summarize research into the contributions of both association and sensory cortex to memory, with the aim of showing how sensory memories can be distributed across cortical regions at all levels of the hierarchy. We will conclude that learning and memory involve the storage of information within the same cortical regions responsible for on-line processing of that information.

### **Memory Mechanisms in Association Cortex**

The most compelling new evidence for how association areas of cortex contribute to memory has come from electrophysiological studies in monkeys performing memory tasks. The objective of such investigations is to ascertain how the responses of neurons in particular cortical areas change while the animal learns some

specified information, or to identify patterns of responses that correlate with recalling that information. An example is the work of Miyashita and colleagues. They recorded responses among neurons in the inferior temporal (IT) cortex of monkeys learning associations between pairs of shapes. Many neurons gave strong responses only when the monkey viewed one particular shape (the “preferred” shape for that neuron), indicating that the responses of these neurons encoded something about the identity of specific shapes. Before training, two shapes (A and B) were selected such that A was a preferred shape and B was not. Shape B then was used as a cue for shape A. The important observation was that, as the monkeys began to learn the cue-shape association, these neurons began to respond to the cue as well (Naya et al., 1996); they developed a response not only to their preferred shape, but also to the cued memory of that shape.

More recently, the same group has studied the flow of information across the cortex during the cued “memorial” responses described above by making simultaneous recordings from two areas in IT cortex—area TE and the perirhinal cortex just anterior to TE. Neurons in TE responded *before* the perirhinal neurons when the monkeys viewed the preferred shape, consistent with the posterior-to-anterior flow of visual sensory information; but the TE neurons responded *after* the perirhinal neurons on trials when the monkeys viewed the cue for the preferred shape, indicating an anterior-to-posterior flow of information during memory recall (Naya et al., 2001). These researchers subsequently identified the frontal cortex as the source of the information flow during cued recall (Tomita et al., 1999; see Figure 1 for description of the experiment).

### **Memory Mechanisms in Sensory Cortex**

From the experiments summarized above, there remains little doubt as to the contribution of association cortex to the formation of sensory or perceptual memories. Evidence is emerging, however, that the network involved in memory storage and retrieval extends to the “early” sensory cortical regions once thought to contribute to the representation of sensory information only in the presence of the stimulus itself. This view is supported by recent studies showing that neuronal discharge patterns in primary sensory cortex can be an essential component of the replay or retention of perceptual events *even in the absence of the external input that originally evoked the perceptual experience*. The most important evidence comes from functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies in subjects performing mental imagery in the absence of external sensory input. For example, in two experiments investigating visual imagery (Kosslyn et al., 1995, 1999), subjects studied novel visual stimuli and later, with eyes closed, were required to make decisions about particular features of these stimuli. PET scanning during recall revealed activation of primary visual cortex (V1). Moreover, the spatial extent of V1 activated in this task was systematically related to the size of the stimulus being remembered (Kosslyn

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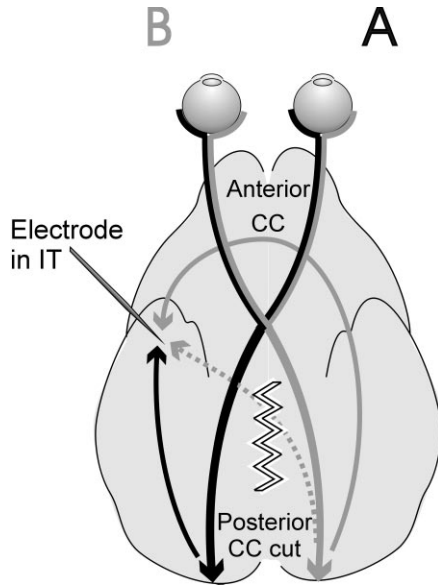


Figure 1. Role of the Frontal Cortex in Cued Memory Recall

The figure illustrates the study by Tomita et al. (1999) in which they recorded neuronal activity in the inferior temporal (IT) cortex of monkeys. Some neurons in IT responded preferentially when the monkey viewed a particular shape (A in this example) presented in the contralateral hemifield. The same neurons also began to respond to a second shape (B) as the monkey learned that it served as a cue for A, suggesting that these responses constituted part of the cued memory of A. Since the cued responses were recorded even when B was presented in the ipsilateral hemifield, it is likely that information about the cue crossed the corpus callosum (CC) in order to reach IT. The researchers then cut the posterior CC, preventing the “bottom up” passage (broken gray line) of information between hemispheres. Despite this, the monkeys continued to retrieve the memory of A when B was presented in the ipsilateral hemifield, and many IT neurons continued to respond to ipsilateral presentations of B. In this case, information about the cue could only reach IT via a longer “top-down” route through the frontal lobes and anterior CC (unbroken gray line). Indeed, the IT neurons responded to B with much longer latencies, confirming that the information was now conveyed via a longer route through the frontal lobes. The role of top-down input from the frontal cortex was confirmed when subsequent transection of the anterior CC eliminated the longer-latency responses in IT neurons and rendered the monkeys incapable of remembering the correct cue-shape associations.

et al., 1995), consistent with an engagement of neuronal processing within the framework of the V1 retinotopic map. Other fMRI studies have shown that visual cortex is not the only sensory cortical area activated during recall of perceptual memories. In one study, the same zone of primary somatosensory cortex was activated when subjects tapped a finger or when they later imagined tapping their finger (Porro et al., 1996). Further, auditory cortical areas were activated when subjects viewed pictures in silence if the pictures had been explicitly paired with particular sounds beforehand (Nyberg et al., 2000; Wheeler et al., 2000). A similar cross-modal activation of auditory cortical areas (including primary auditory cortex) has been observed during silent lip-reading (Calvert et al., 1997).

The above evidence should not be taken to mean that primary sensory cortices are the only areas active during perceptual remembering (e.g., Kreiman et al., 2000;

O’Craven and Kanwisher, 2000). Moreover, there is evidence that primary sensory cortical areas are not always activated by perceptual memory tasks (Roland and Gulyas, 1995), although many of the negative results were collected using less sensitive imaging methods than those now available. This suggests that additional evidence is required in order to understand the contribution of sensory cortex to the formation and recall of perceptual memories. One way to demonstrate a critical role of sensory cortex is to show that memory retrieval is impaired by functional lesion of that area. Such a demonstration has been provided by Kosslyn’s group. They showed that temporary disruption of V1 by transcranial magnetic stimulation impaired subjects’ abilities to imagine stimuli, just as it affected their ability to see those stimuli (Kosslyn et al., 1999).

Still, this approach cannot be used to investigate the role of sensory cortex in *recognition* memory because it would be impossible to determine whether the lesion affected the memory process itself, or simply blocked the relay of sensory information to later cortical areas that might underlie the memory process. An alternative means to investigate the contribution of sensory cortex to memory, circumventing the interpretive complications of lesions, is to examine how memories are spatially distributed with respect to the sensory organ. A striking characteristic of sensory cortical areas, in particular “early” sensory regions, is their topographic organization—the neuronal representation is arranged as a map of the sensory organ itself. Thus, if memories are stored within topographically organized sensory cortical areas, then access to those memories should be topographically distributed. For example, if subjects acquire some perceptual information using a restricted part of the sensory apparatus (e.g., if the information is only available to a small part of the visual field), their ability to recognize that information should decrease proportionally when the information is presented at locations increasingly distant from the original site. Note this argument depends on the information represented in sensory cortex being nondeclarative, since the ability to express declarative information in verbal form would permit complete access to that information irrespective of the spatial location in which it is presented.

Many findings now support this hypothesis: recognition of perceptual information can be topographically distributed, thus implicating primary sensory cortex. In a popular paradigm (e.g., Dill and Fahle, 1997), human subjects learned to recognize a visual stimulus that was presented repeatedly at a specific retinotopic location. After being trained, subjects only recognized the stimulus if presented at or close to the original location, failing to identify the stimulus when it was displaced by as little as 0.7°. In several studies of this type, subjects also failed to recognize the stimulus if it was rotated or was larger or smaller than the training stimulus. These properties strongly implicate early areas of visual cortex (e.g., V1), since neurons in these areas have the requisite retinotopic, orientation, and size selectivity to account for these results. However, the specificity of learning—how readily it transferred to stimuli different from the trained one—was directly proportional to the difficulty of task: when the conditions of the task were very difficult, the subjects only recognized the stimulus at the

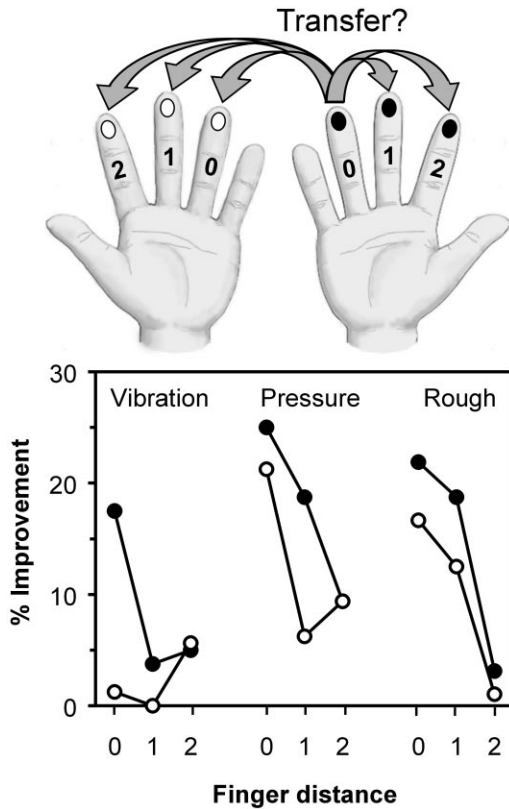


Figure 2. Role of Stimulus Features in the Spatial Distribution of Tactile Perceptual Learning

We trained human subjects to use a single fingertip (e.g., the right ring finger in the top illustration) to discriminate between two stimuli: two vibrations of different frequency, two punctate stimuli (von Frey hairs) of different pressure, or two surfaces of different roughness (Harris et al., 2001). They were then tested for transfer of learning to other fingertips on the same hand (the filled circles in the graph) and on the opposite hand (empty circles). The learning, shown here as the percent improvement in accuracy above the pretraining baseline score, was topographically distributed for all three types of tactile stimulus, and this distribution varied according to stimulus type. There was greater transfer beyond the trained finger for the pressure and roughness discriminations than for vibration; in the latter case there was no benefit of training for any fingertip besides the trained one.

trained position and orientation, but when the task was relatively easy, the subjects' performance generalized to other positions or orientations (Ahissar and Hochstein, 1997). This suggests that early sensory cortex (in this case, V1) is most essential for learning fine discriminations. In keeping with this conclusion, Kosslyn et al. (1995) have suggested that the contribution made by sensory cortex is in the retrieval of detailed metric information about sensory stimuli (e.g., the local geometry of a visible object), information that may be represented within topographic maps.

Recently, we demonstrated that perceptual learning in the tactile modality can be topographically distributed just as it is in vision (Harris et al., 2001; see Figure 2). In our experiments, the storage of tactile information was spatially localized in a way that is best accounted for by the topographic organization of somatosensory

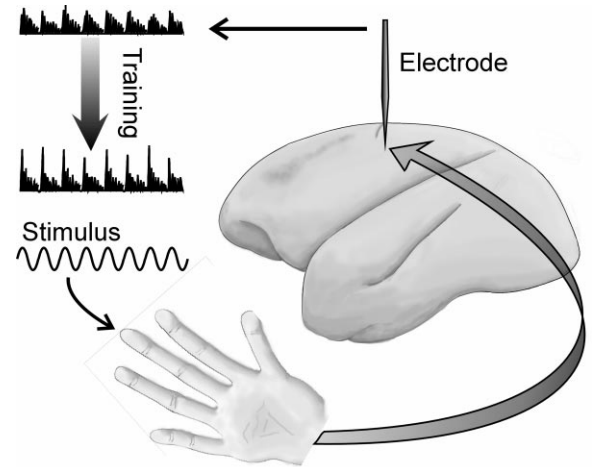


Figure 3. Effects of Perceptual Learning on Neuronal Responses to a Tactile Stimulus

The cartoon portrays the study by Recanzone et al. (1992) in which they recorded from neurons in primary somatosensory cortical area 3b in monkeys that learned to discriminate between vibrations of different frequency delivered to a fingertip. Two types of reorganization occurred. First, there was a dramatic expansion of the cortical territory activated by application of vibratory stimuli to the trained skin site (not depicted here). Second, for the summated population of neurons responding to the vibration, spike times became more sharply phased locked relative to stimulus cycles. Neither of these changes were observed for stimuli applied to a control skin site. The increased temporal fidelity of stimulus representation in cortex paralleled the improved psychophysical performance of individual animals, and signal detection theory indicated that the changes in neuronal temporal response precision could account for the perceptual improvement. Moreover, in a similar study (Wang et al., 1995), no changes in neuronal response were detected in the thalamus, arguing that somatosensory cortex, and not subcortical structures, was the site of the neuronal modifications underlying the learning.

cortex. Moreover, we found differences in the topographic distribution for different types of tactile stimulus. This observation bears on a further implication of the "topographic learning" principle: since sensory cortex is parcelled into multiple areas, each specialized to process specific types of stimuli, the spatial distribution of stored information should reflect the somatotopy present in the cortical area that processes that type of stimulus. Thus, the differences in somatotopy of learning for different stimulus types suggests that the information is stored in stimulus-specific cortical fields, each characterized by a unique receptive field organization, feature selectivity, and callosal connectivity.

More direct support for the assertion that the spatial distribution of perceptual learning derives from the topographic organization of sensory cortex comes from our demonstration of topographic tactile learning in rats (Harris et al., 1999). Rats learned a cortex-dependent detection task using just one whisker and were then tested on that task with a prosthetic whisker attached to the stub of the same or a different whisker. Performance decreased systematically as the distance between the trained and tested whisker sites increased. Moreover, large-scale electrophysiological recordings showed that the extent to which learning transferred across whisker positions was dictated by the degree of overlap between

the representations of those whiskers in primary somatosensory cortex.

The phenomenon of topographically localized memory is best explained by the following model. During perceptual learning, a critical component of the relevant sensory information is stored within a restricted region of the topographic map by the same neuronal population that processes the sensory signal during training. Subsequent performance on the task is proportional to the extent to which the topographic region activated by the new sensory signal overlaps the region where the sensory information has been stored. Thus, sensory experiences endowed with behavioral importance can leave a long-lasting trace in the topographically matched territory of primary sensory cortex. If this conclusion is correct, it should be possible to identify specific changes in the representation of sensory information in primary cortical areas across the course of perceptual learning. Michael Merzenich and colleagues have done exactly that (Recanzone et al., 1992; Wang et al., 1995). They recorded from populations of neurons in primary somatosensory cortex of monkeys that had been trained to detect differences in the frequency of vibrotactile stimuli, and they showed that training increased the number of cortical neurons that responded to the vibration and sharpened the temporal coupling of the responding population to the indentation cycles of the vibration (see Figure 3).

### Conclusions

Recent investigations are allowing precise statements to be made about where in the cortex sensory memories are stored and retrieved. After highlighting new work that has refined the long-recognized contributions of frontal and temporal association areas, this review turned to sensory cortex and suggested that its role in the storage of sensory information and in the retrieval of perceptual memories is not qualitatively different from that played by "later" association areas. In particular, we presented evidence that neuronal activity in sensory cortex contributes to remembering the sensory features of a stimulus. Studies in species as different as humans and rats show that learned recognition of elemental stimulus features can be strictly localized in a way that is best accounted for by information storage within the framework of sensory cortical maps. Finally, electrophysiological studies in monkeys have shown that learning to recognize a stimulus is based on distinct changes in the patterns of neuronal activity in sensory cortex. Thus, each functional region of cortex appears to carry out the dual functions of information processing and information storage. Storage and retrieval involve the very populations of cortical neurons that explicitly encode the relevant information, ensuring that the stored and recalled information is of comparable quality to the information present during on-line processing.

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