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REVIEWS

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WORKING MEMORY IN PRIMATE SENSORY SYSTEMS

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Abstract

Sensory working memory consists of the short-term storage of sensory stimuli to guide behaviour. There is increasing evidence that elemental sensory dimensions — such as object motion in the visual system or the frequency of a sound in the auditory system — are stored by segregated feature-selective systems that include not only the prefrontal and parietal cortex, but also areas of sensory cortex that carry out relatively early stages of processing. These circuits seem to have a dual function: precise sensory encoding and short-term storage of this information. New results provide insights into how activity in these circuits represents the remembered sensory stimuli.

Summary

- Psychophysical, physiological and imaging studies of sensory working memory support the idea that elemental sensory dimensions are represented by distinct memory systems that are likely to include the same cortical areas as those involved in encoding stimulus features.
- In visual psychophysics, this idea is supported by the differences in the length of time for which specific stimulus features are retained, and by studies that use a 'memory masking' approach in which an interaction between an interference stimulus during the memory delay and the preceding stimulus reveals the nature of the remembered stimulus. Memory masking is most effective early in the delay and its effect is specific to the stimulus attributes that are retained. Studies of memory for motion show that the remembered stimuli are spatially localized, indicating the involvement of areas with fairly precise retinotopy, and also show that the spatial scale of the mechanism that underlies performance matches the receptive field size of cortical area MT. Other studies also indicate a separate representation in memory of simple stimulus dimensions such as spatial frequency, orientation and speed.
- Single-cell recordings in monkeys and imaging studies in humans also reveal memory-related activity in regions of visual cortex that are known to process various attributes of visual stimuli (for example, areas IT, V4 and MT). Lesions of areas MT/MST in monkeys and of analogous regions in humans also produce memory-related deficits in motion discrimination. The involvement of visual cortical areas in

retention of visual information is also supported by microstimulation experiments in monkeys and transcranial magnetic stimulation (TMS) in humans.

- Psychophysical studies of tactile working memory show robust and selective retention of tactile signals, implicating the involvement of the regions that process these signals. Physiological recordings reveal memory-related delay activity at the earliest stages of processing of tactile information in S1 for texture and in S2 for vibration discrimination. Imaging studies also show activation of somatosensory regions in cortex during working memory tasks, and TMS applied to S1 during the delay in the vibration discrimination task disrupted performance.
- Psychophysical studies of auditory working memory indicate that elementary dimensions, such as frequency, intensity and sound location, are stored by separate modules. Single-cell recordings in primary auditory cortex during the memory delay show activity that carries information about the remembered tone frequency. The involvement of auditory cortex in working memory for sound is also supported by magnetoencephalography, imaging and lesion studies in humans.
- This review provides evidence for participation of sensory cortical areas in the circuitry that temporarily stores sensory information. However, the precise nature of this participation is still unclear. The use of quantitative sensory psychophysics in conjunction with recording and imaging studies will bring us closer to an understanding of how the brain deals with sensory storage.