Behavioural Brain Research 236 (2013) 67–77

Contents lists available at SciVerse ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Review

Transcranial magnetic stimulation of visual cortex in memory: Cortical state, interference and reactivation of visual content in memory

Vincent van de Ven*, Alexander T. Sack

Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, Maastricht, P.O. Box 616, 6200 MD, The Netherlands

HIGHLIGHTS

- We review TMS evidence that visual cortex plays a causal role in memory for visual events.
- Memory retention and consolidation alter cortical functional state of visual cortex.
- TMS can reactivate visual memory content in occipital cortex and hMT+ into awareness.
- Visual cortex contains a topographically organized neural representation of sensory information in memory.
- The neural mechanism of memory in visual cortex may be similar for different memory systems.

ARTICLE INFO

Article history:
Received 12 July 2012
Accepted 1 August 2012
Available online 19 August 2012

Keywords:
Visual memory
Transcranial magnetic stimulation (TMS)
Visual cortex
Cortical state
Reactivation
Short-term memory
Perceptual learning
Phosphenes

ABSTRACT

Memory for perceptual events includes the neural representation of the sensory information at short or longer time scales. Recent transcranial magnetic stimulation (TMS) studies of human visual cortex provided evidence that sensory cortex contributes to memory functions. In this review, we provide an exhaustive overview of these studies and ascertain how well the available evidence supports the idea of a causal role of sensory cortex in memory retention and retrieval. We discuss the validity and implications of the studies using a number of methodological and theoretical criteria that are relevant for brain stimulation of visual cortex. While most studies applied TMS to visual cortex to interfere with memory functions, a handful of pioneering studies used TMS to 'reactivate' memories in visual cortex. Interestingly, similar effects of TMS on memory were found in different memory tasks, which suggests that different memory systems share a neural mechanism of memory in visual cortex. At the same time, this neural mechanism likely interacts with higher order brain areas. Based on this overview and evaluation, we provide a first attempt to an integrative framework that describes how sensory processes contribute to memory in visual cortex, and how higher order areas contribute to this mechanism.

Contents

1. Introduction 68
2. Considerations in this review 68
   2.1. Structuring of the review 68
   2.2. Positioning the TMS coil over visual cortex 68
3. Memory interference 69
   3.1. Short-term memory 69
   3.2. Memory retention and mental imagery 71
   3.3. Perceptual learning 72
4. Memory reactivation 73
5. Discussion 74
   Acknowledgement 75
   References 75

* Corresponding author. Tel.: +31 43 3884510; fax: +31 43 3884125.
E-mail address: v.vandeven@maastrichtuniversity.nl (V. van de Ven).

0166-4328 © 2012 Elsevier B.V. Open access under CC BY-NC-ND license.
http://dx.doi.org/10.1016/j.bbr.2012.08.001

1. Introduction

Traditionally, the brain's neural systems that retain perceptual experiences in memory are considered to be independent and architecturally non-overlapping with those that encode the sensory information [1–3]. Neurophysiological [4,5] and functional neuroimaging studies [6–11] have shown that memory retention and formation is associated with increased activity in mammalian prefrontal and parietal cortex, with little evidence for activity in sensory areas beyond the initial sensory stimulation. However, this classic notion is now met with controversial findings that show that sensory cortex plays a role in memory processing [12–14]. Several neurophysiological studies showed increased brain activity in visual cortex during the short-term retention of visual information, well after stimulus presentation [15–17]. Further, retrieval of episodic memories can activate modality-specific sensory cortex [18], and structural damage to visual cortex may lead to amnesia of visual memories [19], suggesting that visual cortex is involved in long-term memory storage. These and other findings suggest that, rather than being a reflexive encoding mechanism of sensory information, visual cortex is actively involved in memory consolidation and retrieval.

The correlational nature of the majority of these studies prevents a causal inference of sensory cortex activity in memory functions. To address causality in brain–behavior relations requires the experimental manipulation of brain activity and measure memory performance as a consequence. A classic example of such an approach are the studies by Penfield and co-workers [20,21], who intracranially stimulated sensory cortex in patients who were to undergo brain surgery. They found that stimulation of sensory cortex resulted in reactivation of autobiographical memories in the respective sensory modality, to a perceptual degree that closely resembled real-life sensory experiences. Clearly, the invasive nature of the measurement and recruitment of specific patient populations limits the broad application of this procedure. Transcranial magnetic stimulation (TMS) has proved to be a useful alternative to achieve localized brain stimulation in healthy participants [22–24]. In TMS, biphasic current flow through one or more coils of wire generates a magnetic pulse. Positioning the TMS coil over a position on the scalp allows delivery of the magnetic pulse to the cortical tissue underneath the coil, which locally alters electrical current flow in the neural tissue. This method can thus be used to experimentally test the functional role of sensory cortex in particular memory functions, or probe the criteria under which sensory cortex is functionally relevant to memory.

Following the classic memory-perception division, TMS has been applied to sensory cortex to study perception [25,26], and to higher order regions, such as lateral prefrontal and posterior parietal cortex, to study memory functions (e.g., [27–30]). Comparatively little work addresses how sensory cortex contributes to memory. However, the scientific interest in this topic is rapidly increasing. In this review, we discuss how TMS can be used to study this issue. We illustrate how different TMS protocols can be used to probe the functional contribution of visual cortex in memory retention and consolidation, and memory retrieval. An important consideration is that the available studies present a large heterogeneity of memory paradigms to investigate explicit and implicit memories at shorter and longer time scales. This heterogeneity precludes casting the review according to a particular memory model. Instead, we opted for an empirical approach, in which we discuss a more general mechanism of how sensory cortex contributes to memory formation and retrieval. We speculate on how memory mechanisms in sensory cortex are shared between different memory systems, and how they contribute to memory formation at different time scales. We think that our approach appreciates the value of the TMS studies of memory in sensory cortex, and provides a parsimonious platform to synthesize the findings and derive future hypotheses for testing.

2. Considerations in this review

2.1. Structuring of the review

In this review we adopt an empirical approach to discuss the currently available literature. Table 1 lists the studies that are discussed in this review. Most studies use a 'learning by breaking' approach, in which TMS pulses are administered in order to interrupt neural functioning of the targeted area, thereby interfering with information processing and resulting in worsened cognitive performance. If memory retention requires activity in visual cortex, then a TMS pulse that alters brain activity in visual cortex will interrupt retention, leading to decreased memory performance. This approach has been used to study the contribution of visual cortex to implicit and explicit memory retention and consolidation on shorter and longer time scales.

In addition, TMS has also been used as a way to 'reactivate' visual content in memory into awareness (see Table 1). The handful of pioneering studies conducted so far demonstrate that TMS is especially suited for this approach, in which visual memory content is made available to awareness by inducing artificial sensory experiences, or phosphenes. A useful characteristic of phosphenes is that they reflect functional properties of the stimulated area [31–33]. For example, phosphenes induced with occipital TMS are observed in the visual field contralateral to the side of stimulation, and their visual field position follows the positioning of the coil over the scalp in a retinotopic fashion [33]. Phosphenes induced by TMS over central and lateral occipital sites are typically stationary, and can be of a particular color, shape or brightness. Phosphenes induced with TMS over the human motion complex (hMT+) exhibit localized movement [34,35]. Reactivation studies utilize this property of phosphenes to 'unveil' the current neural representation or 'brain state' of sensory cortex during memory retention or retrieval phases. In turn, these results provide further insight into the neural memory representations in visual cortex.

2.2. Positioning the TMS coil over visual cortex

An important factor in increasing the probability of finding an effect of TMS on behavior is how well TMS targets the cortical locus of interest [36,37]. Here, the strategy of coil positioning over the scalp may be crucial in attaining a strong behavioral effect. The most straightforward approach is to place the coil at the scalp position relative to the inion, an anatomical landmark on the scalp. Many researchers have used this approach to target the cortical representation of central (foveal) vision, or, with a more lateral positioning, to target one of the two hemifields (Fig. 1A). Based only on scalp coordinates, this approach ignores the large inter-individual variability in occipital cortical morphology and functional-anatomical mapping [38]. A more dynamic approach, and unique to TMS of visual cortex, is to induce phosphenes with TMS at different positions over the scalp in order to identify optimal coil position (Fig. 1B). The retinonotopic behavior of occipitally-induced phosphenes can be utilized to position the TMS according to the visual field location of the phosphenes [39–41], while moving phosphenes indicate stimulation of hMT+ or other cortical areas relevant for motion perception [34,35,42]. Importantly, phosphene localization requires subjective reports, and the probability of reliably seeing phosphenes differs across individuals, resulting from individual differences in cortical morphology, functional-anatomical mapping, the distance between scalp and cortex that the magnetic field must bridge and other