NeuroImage 142 (2016) 583–589

Contents lists available at ScienceDirect

NeuroImage

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

Multiple foci of spatial attention in multimodal working memory

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ARTICLE INFO

Article history:
Received 15 May 2016
Accepted 9 August 2016
Available online 17 August 2016

Keywords:
Selective attention
Multisensory (touch/vision)
Working memory (WM)
Event-related potentials (ERPs)

ABSTRACT

The maintenance of sensory information in working memory (WM) is mediated by the attentional activation of stimulus representations that are stored in perceptual brain regions. Using event-related potentials (ERPs), we measured tactile and visual contralateral delay activity (tCDA/CDA components) in a bimodal WM task to concurrently track the attention-based maintenance of information stored in anatomically segregated (somatosensory and visual) brain areas. Participants received tactile and visual sample stimuli on both sides, and in different blocks, memorized these samples on the same side or on opposite sides. After a retention delay, memory was unpredictably tested for touch or vision. In the same side blocks, tCDA and CDA components simultaneously emerged over the same hemisphere, contralateral to the memorized tactile/visual sample set. In opposite side blocks, these two components emerged over different hemispheres, but had the same sizes and onset latencies as in the same side condition. Our results reveal distinct foci of tactile and visual spatial attention that were concurrently maintained on task-relevant stimulus representations in WM. The independence of spatially-specific biasing mechanisms for tactile and visual WM content suggests that multimodal information is stored in distributed perceptual brain areas that are activated through modality-specific processes that can operate simultaneously and largely independently of each other.

Introduction

Information that is no longer physically present, but needed for ongoing behavior, is temporarily stored in working memory (WM). The neural basis of WM involves multimodal brain regions such as prefrontal cortex (PFC, Curtis and D'Esposito, 2003; Fuster and Alexander, 1971; Postle, 2006; Sreenivasan et al., 2014) and posterior parietal cortex (PPC, Xu and Chun, 2006), as well as modality-specific perceptual brain areas (Pasternak and Greenlee, 2005; Supèr et al., 2001; Zhou and Fuster, 1996). According to the sensory recruitment model of WM (Jonides et al., 2005), cortical regions that have encoded sensory signals into WM also mediate the short-term storage of these signals. This hypothesis is supported by fMRI and EEG experiments demonstrating that stimulus-specific WM content can be decoded from neural activity in sensory cortex (Emrich et al., 2013; Harrison and Tong, 2009). Higher-level cortical areas, such as the PFC, which assert top-down influence on perceptual areas are thought to regulate the maintenance of task-relevant stimulus representations in sensory cortex (Awh and Jonides, 2001; Awh et al., 2006; Curtis and D'Esposito, 2003; Postle, 2006; Sreenivasan et al., 2014), but these higher brain regions may also play a role in information storage (Riley and Constantinidis, 2016; Romo and Salinas, 2003; Ester et al., 2015; Mendoza-Halliday et al., 2014).

The attention-based maintenance of WM representations is thought to be governed by a single supramodal control system that operates across all sensory modalities (Cowan, 2011; Cowan et al., 2011). However, this type of supramodal attentional control may be difficult to reconcile with the sensory recruitment model. If the storage of sensory information in working memory is based on the recruitment of perceptual brain areas, the maintenance of this information may also be mediated by modality-specific attentional processes. For example, tactile and visual WM representations have different spatial layouts, because they were encoded into WM by sensory neurons whose receptive fields are organized in a modality-specific fashion (somatotopic versus retinotopic; Katus et al., 2015b; Golomb et al., 2008; Golomb and Kanwisher, 2012). Hence, spatially selective processes that direct focal attention to WM content should rely on such modality-specific coordinate systems, as these index the locus where sensory information is stored in the brain. The top-down attentional control of working memory in different modalities can be investigated in multimodal WM tasks that require the concurrent maintenance of tactile and visual stimuli. In such tasks, distinct foci of tactile and visual spatial attention may emerge simultaneously over somatosensory and visual cortex. However, the hypothesis that spatially selective processes bias modality-specific (tactile/visual) WM representations simultaneously, and perhaps even independently, has so far never been tested empirically.

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http://dx.doi.org/10.1016/j.neuroimage.2016.08.019
1053-8119/

Previous event-related potential (ERP) studies have uncovered distinct electrophysiological correlates of the attention-based maintenance of visual and tactile WM representations. The contralateral delay activity (CDA) emerges during the retention of visual stimuli over posterior visual areas contralateral to the visual field in which memorized items had been presented (Vogel et al., 2005; Vogel and Machizawa, 2004). The CDA is sensitive to WM load and individual differences in WM capacity, and reflects the spatially selective maintenance of information in visual WM. The tactile CDA component (tCDA) shows a similar response profile as its visual counterpart, but has a modality-specific topography over contralateral somatosensory cortex (Katus and Eimer, 2015; Katus et al., 2015a; Katus and Müller, 2016; for further discussion of the relationship between the tCDA and the somatotopic organization of tactile WM, see Katus et al., 2015b). So far, the CDA and tCDA components have been investigated exclusively with unimodal (visual or tactile) WM tasks. For the first time, we here concurrently measured the tCDA and CDA components in a bimodal WM task to track the maintenance of tactile and visual WM representations simultaneously. To distinguish between the tCDA and CDA, we used current source density (CSD) transforms (Tenke and Kayser, 2012), which minimize volume conduction effects between these components. Note that both the tactile and visual CDA are inherently spatially selective markers of WM maintenance, because these lateralized components are isolated by subtracting ipsilateral from contralateral ERPs (as defined relative to the side where stimuli are memorized). We therefore employed a spatial manipulation to examine whether the spatially selective biasing of tactile and visual WM representations is mediated by dissociable processes.

Bimodal (tactile/visual) sample sets were simultaneously presented on the left and right sides (Fig. 1). Participants memorized the locations of two tactile stimuli and the colors of two visual stimuli, before memory was unpredictably tested for vision or touch. The location where the task-relevant visual and tactile sample stimuli had to be retained alternated across experimental blocks. In half of all blocks, participants memorized tactile and visual stimuli on opposite sides (touch left/vision right, or vice versa). In the other half, their task was to memorize tactile and visual stimuli on the same side. If distinct spatially selective biasing mechanisms maintain focal attention on tactile and visual memory representations, the tCDA and CDA components should emerge over opposite hemispheres in opposite sides blocks, whereas in same sides blocks, both components should manifest over the same hemisphere. The tCDA/CDA components should be statistically reliable (as indexed by amplitudes that differ from zero), and importantly, the polarities of these components should differ between same and opposite sides blocks. Such a pattern of results would strongly support the hypothesis that separate spatially selective biasing mechanisms maintain focal attention on stimulus representations that were encoded into WM through different modalities.

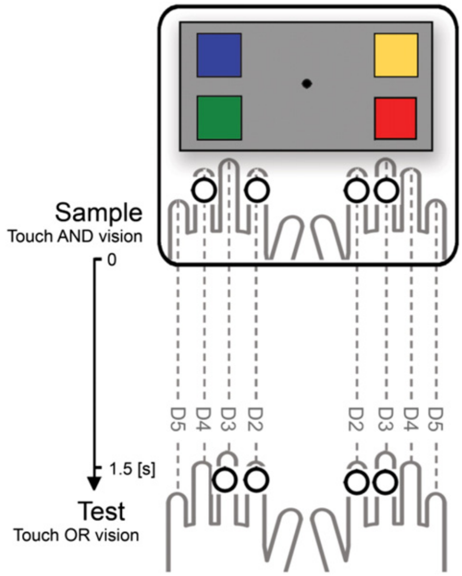

Fig. 1. Stimulation procedure and task. A bimodal (tactile–visual) sample set was followed after 1.5 s by a unimodal test set (unpredictably tactile or visual). The locations of the tactile sample stimuli (indicated by circles) were memorized on one task-relevant hand (left or right), and the colors of the visual stimuli were memorized in one visual field (left or right). In *same side* blocks, tactile and visual sample stimuli were memorized on the same side. In *opposite side* blocks, participants memorized tactile samples on the left hand and visual samples on the right side, or vice versa. In each trial participants reported a match or mismatch between sample and test sets (on the task-relevant hand/side).

Materials and methods

Participants

Twenty neurologically unimpaired paid adult participants took part in the experiment. One participant was excluded due to poor behavioral performance (memory accuracy for tactile stimuli was below 60%), another because of excessive alpha activity. The remaining eighteen participants (mean age 29 years, range 19–42 years, 11 female, 17 right-handed) all had normal or corrected vision. The study was conducted in accordance with the Declaration of Helsinki, and was approved by the Psychology Ethics Committee, Birkbeck College. All participants gave informed written consent prior to testing.

Stimulation hardware and stimulus materials

Participants were seated in a dimly lit recording chamber with their hands covered from sight. Tactile stimuli were presented by eight mechanical stimulators that were attached to the left and right hands' distal phalanges of the index, middle, ring and small fingers. The stimulators were driven by custom-built amplifiers, controlled by MATLAB routines (The MathWorks, Natick, USA) via an eight-channel sound card (M-Audio, Delta 1010LT). Tactile stimuli were presented in sets of four simultaneous pulses (two to each hand), consisting of 100 Hz sinusoids that were presented for 150 ms with an intensity of 0.37 N. Headphones presented continuous white noise to mask any sounds produced by tactile stimulation.

Visual stimuli were shown for 150 ms at a viewing distance of 100 cm against a black background on a 22 inch monitor (Samsung SyncMaster 2233; 100 Hz refresh rate, 16 ms response time). Four differently colored squares were presented simultaneously (one in each quadrant). Each square had a size of 0.63° of visual angle, and all squares were equidistant from central fixation, with a horizontal eccentricity of 0.64° and a vertical eccentricity of 053° of visual angle (measured relative to the squares' centers). Six equiluminant colors (11.8 cd/m^2) were used in the experiment (red, green, blue, yellow, cyan and magenta). A white fixation dot was constantly present on the screen centre throughout the experiment. At the end of each trial, a question mark was shown centrally for 2000 ms to indicate the response period.

Stimulation procedure and task

We used a bimodal WM procedure that combined two lateralized change detection tasks for tactile and visual stimuli. Fig. 1 illustrates the stimulation procedure. Bimodal (tactile and visual) sample sets were followed after 1500 ms by a unimodal test set (tactile or visual, 50%). The sample sets included two visual stimulus pairs on the left and right side of the monitor, and two tactile stimulus pairs, presented simultaneously to the left and right hands. Participants were instructed to memorize visual and tactile stimulus pairs on one task-relevant side, and to decide whether the (tactile or visual) test stimulus set matched the memorized sample set on the respective task-relevant side. In