NeuroImage 174 (2018) 153–163

Contents lists available at ScienceDirect

NeuroImage

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

Persistent recruitment of somatosensory cortex during active maintenance of hand images in working memory

A. Galvez-Pol[a,b,*,1], B. Calvo-Merino[a,**,1], A. Capilla[c], B. Forster[a]

[a] Cognitive Neuroscience Research Unit, Psychology Department, City, University of London, EC1V 0HB, UK
[b] Sobell Department of Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London, WC1N 3BG, UK
[c] Departamento de Psicología Biológica y de la Salud, Universidad Autónoma de Madrid, 28049, Spain

ARTICLE INFO

Keywords:
Body perception
Sensory recruitment
Working memory
Embodiment
Somatosensory cortex
SEPs

ABSTRACT

Working memory (WM) supports temporary maintenance of task-relevant information. This process is associated with persistent activity in the sensory cortex processing the information (e.g., visual stimuli activate visual cortex). However, we argue here that more multifaceted stimuli moderate this sensory-locked activity and recruit distinctive cortices. Specifically, perception of bodies recruits somatosensory cortex (SCx) beyond early visual areas (suggesting embodiment processes). Here we explore persistent activation in processing areas beyond the sensory cortex initially relevant to the modality of the stimuli. Using visual and somatosensory evoked-potentials in a visual WM task, we isolated different levels of visual and somatosensory involvement during encoding of body and non-body-related images. Persistent activity increased in SCx only when maintaining body images in WM, whereas visual/posterior regions' activity increased significantly when maintaining non-body images. Our results bridge WM and embodiment frameworks, supporting a dynamic WM process where the nature of the information summons specific processing resources.

Introduction

Learning from others is essential in our social culture. This frequently involves perceiving and temporarily maintaining information about others' bodies and actions in memory. This temporary storage of task-relevant information for goal-directed behaviours is known as working memory (Baddeley, 2012; Postle, 2006; Sreenivasan et al., 2014). Working memory (WM) is underpinned by a distributed network of brain areas (Christophel et al., 2017; Postle, 2006). Interestingly, current research postulates that WM storage is achieved by allocating sustained attention to internal and sensory representations of the information (Awh and Jonides, 2001; Carlisle et al., 2011; D'Esposito and Postle, 2015; Gazzaley and Nobre, 2012; Kundu et al., 2013). Examples of this mechanism come from studies showing that maintaining arbitrary images such as colours and polygonal shapes in visual WM elicits neural recruitment in visual occipito-parietal cortices. This recruitment can be observed as a persistent activity that increases with the number of stimuli to-be-remembered during the consolidation interval of the information in WM (Luck and Vogel, 2013; Tsubomi et al., 2013; Vogel and Machizawa, 2004). The evidence for the storage of sensory information within the same areas engaged in its perception has led to the sensory recruitment models of WM (Harris et al., 2002; Pasternak and Greenlee, 2005; Serences et al., 2009; Sreenivasan et al., 2014).

Sensory recruitment models of WM suggest a certain degree of overlap between the neural mechanisms involved in perceiving and maintaining information in memory, and have been supported by studies that usually employed arbitrary images of shapes or colours to-be-remembered. While perceiving these stimuli does not seem to require a multi-regional perceptual process, it is well-described that encoding others' bodies and actions engages fronto-parietal networks including our own body representation in sensorimotor and somatosensory cortex (Caspers et al., 2010; Molenberghs et al., 2012). This latter process has been associated to embodiment accounts, highlighting the importance of our own body and motor representations during the encoding of body-related information (Calvo-Merino et al., 2005; Sel et al., 2014; Urgesi et al., 2007). Importantly, previous behavioural studies that examined WM mechanism for body-related images had already suggested that internal bodily/sensorimotor representations contribute to

---

[*] Corresponding author. Sobell Department of Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London, WC1N 3BG, UK.
[**] Corresponding author. Cognitive Neuroscience Research Unit, Psychology Department, City, University of London, EC1V 0HB, UK.
E-mail addresses: a.pol@ucl.ac.uk (A. Galvez-Pol), b.calvo@city.ac.uk (B. Calvo-Merino), almudena.capilla@uam.es (A. Capilla), b.forster@city.ac.uk (B. Forster).
[1] Equal contribution.

https://doi.org/10.1016/j.neuroimage.2018.03.024
Received 2 October 2017; Received in revised form 23 February 2018; Accepted 12 March 2018

perceive and maintain in memory visually perceived body-related information (Shen et al., 2014; Smyth et al., 1988; Smyth and Pendleton, 1990, 1989; Wood, 2007).

Based on the aforementioned models proposing similar neural mechanisms for perception and memory and the studies showing recruitment of body-related cortices during perception of bodies, we investigated whether the active maintenance of body-related images in WM elicits neural recruitment of visual regions (as previously described for simple images of shapes) and other sensory regions that participate in the representation of body-related information in the brain (i.e., somatosensory cortex, SCx). To this aim, we examined persistent activity (a neural marker of attention based rehearsal) during a WM task for body and non-body-related images. Persistent activity, also known as sustained or delay activity, is usually observed between the memory and test phases (i.e., during the retention interval) in sensory areas relevant for the task. A key feature of this activity is that it persists in the absence of continued sensory input. Moreover, its amplitude is modulated by the number of stimuli to-be-remembered (memory load) (Luria et al., 2016; Todd and Marois, 2004; Vogel and Machizawa, 2004). In the current study, we recorded persistent activity within visual and somatosensory-evoked potentials (VEPs, SEPs) in a visual WM task where participants were instructed to memorise images of hands and matching polygonal shapes (Fig. 1a and c). Similar to previous studies of WM for visually perceived stimuli (McCollough et al., 2007; Tsubomi et al., 2013; Vogel and Machizawa, 2004), we recorded trials containing VEPs elicited by the visual onset of the images to-be-remembered (visual-only trials). Importantly, we also probed the state of SCx by using task-irrelevant tactile taps that were delivered to the participants' fingers in synchrony with the onset of the images to-be-remembered. The resulting activity contained brain activity due to visual and somatosensory-evoked potentials (visual-tactile trials). While the analyses of VEPs from visual-only trials allowed us to examine persistent activity arising from occipito-parietal visual regions, it also enabled us to examine SCx processing by subtracting brain activity of the visual-only trials to the compound activity of the visual-tactile trials (see Sel et al., 2014). This subtraction (Fig. 1b) allowed us to reveal an ERP component that has not been described yet in the WM or action observation literature, a visually driven component in the form of persistent activity reflecting encoding and maintenance of visual information of body images beyond visual areas in SCx.

Materials and methods

Participants

Twenty participants (10 males; mean age = 28.5) with normal or corrected-to-normal vision took part and gave informed consent, approved by City, University of London Psychology Department's Research Ethics Committee. The sample size of the current experiment was based on previous studies using comparable WM paradigms and techniques (e.g., Vogel and Machizawa, 2004; Tsubomi et al., 2013; Katus et al., 2015).

Stimuli

A set of 6 pictures of right hands depicting different postures with no meaning or symbolism was used. These hand images were horizontally mirrored to create left hand images, resulting in 6 pairs of right and left hands that were then greyscaled. For the control condition, a set of greyscaled geometrical shapes matching the hands' outline and size was

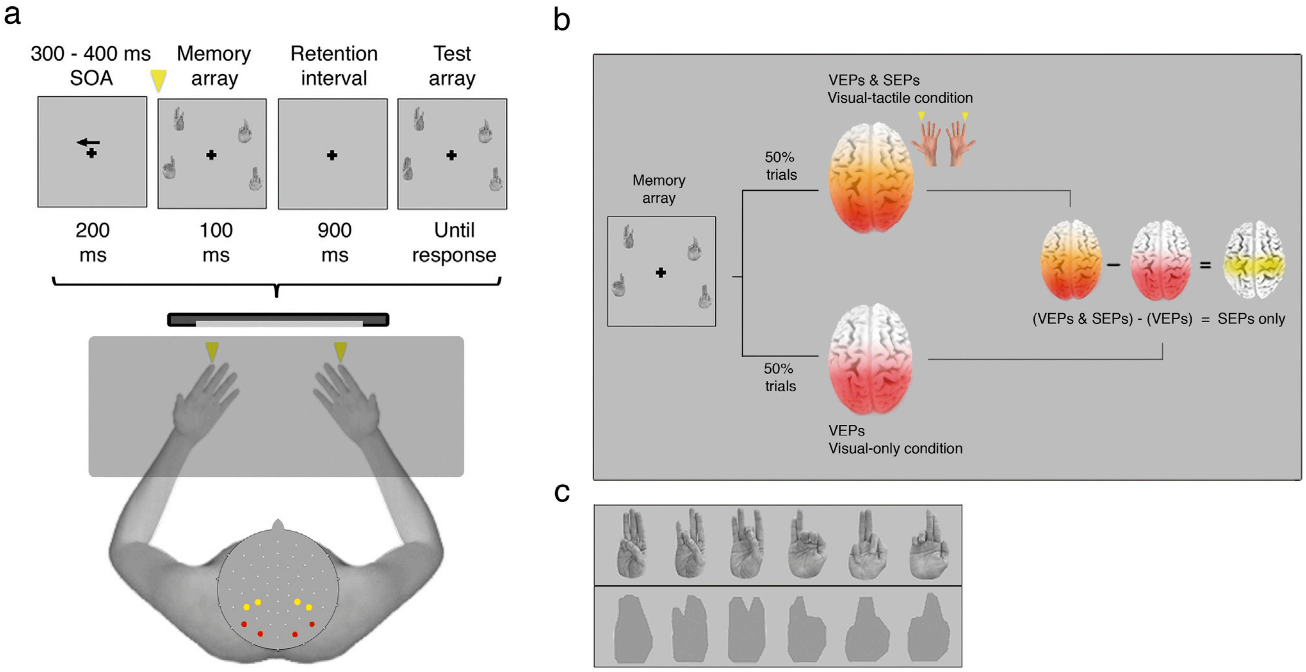

Fig. 1. Task design, schematic illustration of subtractive methodology using SEPs and VEPs, and example of stimuli. (a) All participants performed a WM task for body-related images (hands) and control, non-body-related images (shapes). Participants verbally responded whether or not the stimuli in the left or right hemifield (as indicated by the arrow) were the same in the memory and test arrays. Half of the trials included task-irrelevant tactile stimulation delivered to both index fingertips at the onset of the memory array (yellow triangles). The yellow dots in the mannequin's head indicate the electrode sites included in the analyses of SEPs whereas the red dots indicate the sites analysed for VEPs. (b) Schema of the subtraction methodology employed to isolate SCx processing from visual carry over effects elicited after the perception of the memory array. The visual-tactile condition (50% of trials) included VEPs elicited at the onset of the visual array and somatosensory evoked potentials (SEPs) elicited by task-irrelevant tactile stimulation applied simultaneously at the onset of the visual memory array (central-upper section). The visual-only condition (50% of trials) consisted of only VEPs (central-bottom section) elicited at the onset of the visual array. The subtraction illustrated on the right [visual-tactile condition]-[visual-only condition] allows dissociating SCx from the concurrent visual activity. (c) Example of 6 grey scaled right hands depicting different hand/finger positions and homologous shapes stimuli.