



Modulation of motor cortex activity in a visual working memory task of hand images

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ARTICLE INFO

Keywords:

Motor cortex
Neural recruitment
Embodiment
Working memory
Body perception

ABSTRACT

Recent studies suggest that brain regions engaged in perception are also recruited during the consolidation interval of the percept in working memory (WM). Evidence for this comes from studies showing that maintaining arbitrary visual, auditory, and tactile stimuli in WM elicits recruitment of the corresponding sensory cortices. Here we investigate if encoding and WM maintenance of visually perceived body-related stimuli engage just visual regions, or additional sensorimotor regions that are classically associated with embodiment processes in studies of body and action perception. We developed a novel WM paradigm in which participants were asked to remember body and control non-body-related images. In half of the trials, visual-evoked activity that was time-locked to the sight of the stimuli allowed us to examine visual processing of the stimuli to-be-remembered (visual-only trials). In the other half of the trials we additionally elicited a task irrelevant key pressing during the consolidation interval of the stimuli in WM. This manipulation elicited motor-cortical potentials (MCPs) concomitant to visual processing (visual-motor trials). This design allowed us to dissociate motor activity depicted in the MCPs from concurrent visual processing by subtracting activity from the visual-only trials to the compound activity found in the visual-motor trials. After dissociating the MCPs from concomitant visual activity, the results show that only the body-related images elicited neural recruitment of sensorimotor regions over and above visual effects. Importantly, the number of body stimuli to-be-remembered (memory load) modulated this later motor cortical activity. The current observations link together research in embodiment and WM by suggesting that neural recruitment is driven by the nature of the information embedded in the percept.

1. Introduction

Perceiving and reflecting about others is a crucial aspect of human cognition. On the one hand, perceiving actions, body-tool interactions, and images of body parts engages our own body representations in somatosensory and sensorimotor regions, over and above visual brain areas (Caspers et al., 2010; Molenberghs et al., 2012). These findings have been conceptualised within the embodiment framework, suggesting that the aforementioned activations reflect our ability to process bodily percepts and other stimuli at the sensory, motor, and/or affective levels in the same ways as one's own body (Calvo-Merino et al., 2005; De Vignemont, 2011; Gallese and Sinigaglia, 2011; Sel et al., 2014; Urgesi et al., 2007). On the other hand, reflecting about others also entails the temporary retention of body-related information beyond its immediate physical presence (beyond perception), a process known as working memory (WM). Interestingly, the results of a recent electrophysiological study (Galvez-Pol et al., 2018) suggest the involvement of somatosensory regions, which are highly interconnected

with further sensorimotor cortices, during WM for visually perceived body-related information. Also, earlier behavioural studies indicate the contribution of sensorimotor regions during the encoding and consolidation of visually perceived bodily information in WM (Shen et al., 2014; Smyth et al., 1988; Smyth and Pendleton, 1989; Wood, 2007), however the concomitant neural underpinnings of this phenomenon are unclear.

Current accounts in WM research postulate that brain areas contributing to the perception of information also underpin its consolidation in WM (i.e., sensory recruitment models; D'Esposito and Postle, 2015; Pasternak and Greenlee, 2005; Serences et al., 2009). Evidence for the sensory recruitment models comes from studies showing that maintaining arbitrary stimuli in WM such as coloured squares, auditory tones, and tactile taps elicits persistent activity that is modulated by the number of stimuli to-be-remembered in visual (McCollough et al., 2007; Tsubomi et al., 2013; Vogel and Machizawa, 2004), auditory (Huang et al., 2016), and somatosensory cortices (Harris et al., 2002; Katus et al., 2014), respectively. Here we argue that according to the

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embodiment framework, visual processing (and therefore encoding and maintaining) of socially meaningful stimuli such as body-related images, should recruit sensorimotor regions over and above the sensory-locked activity in early visual cortices.

In the present study we used a stimulus set involving images of hands depicting different postures. For the control non-body-related stimuli, we developed an additional set of polygonal shapes based on the outline of the hands. We matched the discriminability between stimulus conditions in earlier pilot experiments and also report similar discriminability between these stimuli in our latest work in WM (Galvez-Pol et al., 2018). We expect that notwithstanding differences in the appearance of the stimuli (body and non-body-related), memory processing and recorded activity may be driven by conceptual rather than perceptual complexity; which is congruent with previous memory studies (Konkle and Brady, 2010; McWeeny et al., 1987; Brady et al., 2016). Secondly, we developed a novel paradigm that enables investigating activity in visual cortex and motor regions by dissociating sensorimotor activity from concomitant activity due to the visual processing of body-related images in a visual WM task (as opposed to encoding WM maintenance of non-body-related images). This paradigm takes advantage of the lateralized organization of the visual and motor system and two well-known electroencephalographic components indexing visual and motor processing. The first component is the visual contralateral delay activity (vCDA), which refers to a visual-evoked potential in the form of persistent activity that increases with the number of stimuli to-be-remembered in the posterior-contralateral hemisphere to the encoded visual field (Luria et al., 2016; Vogel and Machizawa, 2004). The second component is a motor-cortical potential (MCP) resembling that observed before self-initiated movements in the readiness potential, also known as *Bereitschaftspotential* (Deecke et al., 1976; Smulders and Miller, 2012); a component arising from motor and premotor cortices and known to reflect the underlying processing of one's motor responses, such as the forthcoming complexity of an executed or imagined action (Kranzloch et al., 2010, 2009), as well as others' observed bodily actions (van Schie et al., 2004).

By developing a visual WM paradigm comprising these two well-known neural indexes of visual and motor involvement (CDA and MCPs, respectively), we sought to examine the effects of memory load across visual and more anterior/motor regions. If WM storage is merely based on the sensory modality originally engaged in the perception of the information, the number of body-related stimuli would not influence the MCPs. Crucially, if it operates according to the type of information embedded in the visual domain, the number of body-related stimuli to-be-remembered would modulate the MCPs beyond the visual evoked modulation. Following previous electroencephalography work that isolated superimposed neural generators (Galvez-Pol et al., 2018; Sel et al., 2014; Talsma et al., 2010; Talsma and Woldorff, 2005), in half of the trials we elicited only visual-evoked potentials (visual-only trials), whereas in the other half we elicited both visual-evoked and motor-cortical potentials within each trial (visual-motor trials). This design allows measuring visual activity arising from occipito-parietal visual regions and sensorimotor processing of visual information while diminishing the effect of superimposed visual generators by subtracting brain activity from the visual-only trials to the combined activity of visual-motor trials.

2. Materials and methods

2.1. Participants

Twenty participants (10 females, mean age = 29; age range 19–41 years) with normal or corrected-to-normal vision took part and gave informed consent for this study, approved by City, University of London Psychology Department's Research Ethics Committee. The sample size was chosen based on other ERP studies using delayed match-to-sample paradigms (Katus and Eimer, 2016; Vogel and Machizawa, 2004).

2.2. Stimuli

The stimuli presented in the current study were developed from a larger set of 27 pairs of hand images depicting different postures. The selection criterion was the following: selecting images that did not convey meaning or symbolism (e.g., a fist with the thumb up could be remembered as 'OK'). Similarly, we wanted to avoid participants counting the number of fingers up, therefore, to lessen this strategy all stimuli have 2 or 3 fingers up. Finally, a set of 6 pictures of right hands depicting different hand postures and finger positions with no meaning or symbolism was used (Fig. 1C). These hands were horizontally rotated to the left, obtaining 6 pairs of right and left hands that were then greyscaled. We created a control condition composed by a set of geometrical shapes matching the hands' outline, size, and colour. We piloted these stimuli and made small adjustments to obtain similar discriminability. Our recent work in WM using these stimuli reports similar discriminability (Galvez-Pol et al., 2018).

2.3. Experimental design and procedure

Participants were seated in front of a LCD monitor (75 Hz) in a dimly lit, electromagnetically shielded room. Participants' forearms rested on the top of a table with their hands separated about 25 cm, in palm down position, and covered by a black surface. Participants performed both stimulus conditions (i.e., hands and geometrical shapes) in counterbalanced order. They were instructed to judge differences between pairs of arrays depicting different hand postures or shape forms. At the beginning of each trial a central arrow cue (200 ms) instructed the participants to covertly attend to the items in either the left or the right hemifield. After the offset of the arrow cue (300–400 ms), the memory array was displayed for 100 ms and followed by a blank retention interval (800 ms). At the end of the retention interval the fixation cross changed from red to green until the end of the trial, 100 ms after this colour change the test array was displayed. In the blocks with visual-only trials, participants were instructed to ignore this colour change. In the blocks with visual-motor trials, participants were instructed to prepare a task-irrelevant motor response during the retention interval that had to be executed at the onset of the green fixation cross. This response was done by simultaneously pressing two different keys with the index fingers of both hands. Finally, the test array was displayed until participants verbally responded whether or not the stimuli in the cued hemifield of the test array were identical to the memory array (Fig. 1A). One of the items in the test array differed from the memory array in 50% of the trials; the rest of the stimuli remained the same. All trials were separated by a 700 ms blank interval.

The shape and hand images were displayed using E-Prime Software (Psychology Software Tools). All stimulus arrays were presented within two $6^\circ \times 8.5^\circ$ rectangular regions that were centred 4° to the left and right of a central fixation cross on a light grey background. Each memory array consisted of 1 or 2 hands ($1.4^\circ \times 0.9^\circ$) in each hemifield, each stimulus being randomly selected from the set of twelve hands. Right hands were shown on the right hemifield while left hands were displayed on the left. The rationale behind this latter choice is based on the clear contralateral representation of the hands in the motor cortex. This allows observing contralateral activity over motor regions that can be dissociated from concomitant visually evoked activity when seeing and remembering the stimuli. In the control condition 1 or 2 polygonal shapes ($1.4^\circ \times 0.9^\circ$) were selected and shown in a similar fashion. The positions of all stimuli were randomized on each trial with the restriction that the distance between stimuli within a hemifield was maintained to a minimum of 2.4° (centre to centre). Since previous studies have shown that holding in WM two items may well lead to limits in WM capacity (Alvarez and Cavanagh, 2004; Luria et al., 2010; Wood, 2007) memory load 1 and 2 would allow detecting increased activity related to memory encoding and maintenance of the stimuli. Participants performed a total of 1344 trials, 672 for each stimulus

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