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

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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.

Keywords: motor cortex, neural recruitment, embodiment, working memory, body perception

Highlights

- Isolation of motor-cortical potentials (MCPs) from visual processing of body-related images in WM
- Persistent visual activity modulated by memory load during WM maintenance of body and non-body-related stimuli
- Distinctive modulation of MCPs by memory load only during maintenance of body-related stimuli
- Type of information embedded in visual stimuli summons specific processing resources (embodiment acting upon WM processes)

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 embodiment framework, visual processing (and therefore encoding and maintaining) 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 (Kranczioch 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 (Figure 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 25cm, 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 (200ms) instructed the participants to covertly attend to the items in either the left or the right hemifield. After the offset of the arrow cue (300-400ms), the memory array was displayed for 100ms and followed by a blank retention interval (800ms). At the end of the retention interval the fixation cross changed from red to green until the end of the trial, 100ms 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 (Figure 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 700ms blank interval.

The shape and hand images were displayed using E-Prime Software (Psychology Software Tools). All stimulus arrays were presented within two 6° x 8.5° 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° x 0.9°) 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° x 0.9°) 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 condition (hands and geometrical shapes). This is equal to 336 trials for each memory load condition (load 1 and 2) of which half entailed the memory task irrelevant motor response (visual-motor condition) and the other half visual only trials (visual-only condition). The following experimental manipulations were randomly presented to the participants on trial by trial basis: memory load, side of the cue, and location of the stimuli on the screen. The type of trials (visual-motor and visual-only) were counterbalanced across blocks and the order of the stimulus conditions was counterbalanced across participants.

2.4. EEG recording and data analysis.

Event-related potentials were recorded from 64 Ag/AgCL active electrodes mounted equidistantly on an elastic electrode cap at standard locations of the international 10-10 system (M10 montage; EasyCap GmBH). Electrodes were referenced to the right mastoid and re-referenced to the average reference off-line. Vertical and bipolar horizontal electrooculogram was recorded for eye movements tracking and artifact correction purposes. Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling rate). Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts). The data were digitally low-pass-filtered at 30 Hz, and ocular correction was performed (Gratton et al., 1983). Trials with horizontal eye movements (HEOG exceeding ± 55 µV) or other artifacts (voltage exceeding ± 85 µV at any electrode) were excluded from analyses. The EEG signal was epoched into 1750ms segments, starting 200ms before the memory array of each trial and ending 550ms after the offset of the green fixation cross. This included activity associated with the visual processing of the memory array in the visual-only condition (locked to the visual memory array), and activity associated with both the visual processing of the memory array and the motor response that was elicited by the task irrelevant key pressing in the visual-motor condition. All these segments were corrected relative to the 100 ms prestimulus interval. Following this, grand averages were computed based on correct response trials. The corresponding segments locked to the visual memory array were epoched into 1200ms and the segments comprising response-locked potentials were epoched into 1250ms (-1150ms preceding the motor response to 100ms after).

2.4.1. Visual-evoked potentials (locked to visual memory array)

Grand averages were computed independently for the two stimulus conditions, separately for the two memory loads, and for visual-only trials by averaging brain waveforms elicited at electrodes over the hemisphere contralateral and ipsilateral to the side to be memorized as indicated by the central cue. Then, visual contralateral delay activity (vCDA) was computed from 300 to 800ms after the onset of the visual memory array to-be-remembered as the difference between contralateral amplitudes (averaging evoked potentials over right visual hemisphere when attending left hemifield and over left visual hemisphere when attending the right hemifield) and ipsilateral amplitudes (average of evoked potentials over the right visual hemisphere when attending the right hemifield and *vice versa*) (Luck, 2012). Statistical analysis was performed for mean amplitudes in accordance with sites and time windows reported in previous studies (Vogel et al., 2005; Vogel and Machizawa, 2004), specifically, occipital and posterior parietal electrode sites (midway between POz and PO3, midway between PO7 and P3 / midway between POz and PO4, midway between PO8 and P4 of the 10-20 system). To account for multiple comparisons in the further analyses of mean amplitudes across hemispheres in the vCDA, the significance level was Bonferroni-corrected (corrected *P* values: 0.05/2).

2.4.2. Motor cortical potentials (locked to motor response - MCPs)

The amplitude of MCPs is modulated during movement planning, observation, execution, and motor learning. Previous studies describe a steep modulation of activity approximately half of a second before the onset of voluntary movements, which slope is found over the contralateral motor cortex of the moving hand. The cued MCP employed in the present study resembles partially the volitional/self-initiated Bereitschaftspotential (Cui et al., 1999; Deecke et al., 1976): it follows similar temporal dynamics, however, it involves additional activation in premotor areas (Gerloff et al., 1998; Smith and Staines, 2012).

MCPs were obtained by averaging the elicited activity preceding the task-irrelevant motor response during the retention interval in the visual-motor condition, meaning that they were measured with respect to the moment the participants performed the key pressing (from -1150 to 100 ms, 0 ms being the actual key press). We then compute statistical analysis of MCPs that allowed us to explore our main hypothesis: modulation of neural recruitment in sensorimotor regions depending on the number of hand images to-be-remembered. In accordance to the aforementioned temporal dynamics, as well as electrodes sites used in previous research (Kranczioch et al., 2009; Smith and Staines, 2012; Smulders and Miller,

2012) we defined two regions of interested (ROIs) that were analysed from -500ms to -50ms before the onset of the movement produced in the task-irrelevant motor response. There were two (contralateral and ipsilateral) frontocentral (midway between C1 and FC1/midway between C1 and FC2, FC3/FC4, FC5/FC6) and frontal ROIs (F1/F2, F5/F6, and AF3/AF4) (Figure 1A). We averaged contralateral MCPs (averaging brain activity over right motor hemisphere when attending left hemifield and over left motor hemisphere when attending the right hemifield) and ipsilateral amplitudes (average of evoked potentials over the right hemisphere when attending the right hemifield and *vice versa*). Factors included in the analyses were hemisphere (contralateral, ipsilateral), ROI (frontocentral, frontal), electrode (3 levels), memory load (1,2), and stimulus condition (hand images, shape images).

2.4.2.1 Subtraction of evoked potentials

Importantly, in a WM task using body-related images, the visual-evoked potentials elicited at the sight of these stimuli may spread from posterior to more anterior motor regions, superimposing brain activity from different neural generators (see for instance Galvez-Pol et al., 2018; Ahlfors et al., 2010; Irimia et al., 2012; Luck, 2014), and likely masking activity over motor cortices that may resonate with the number of body-related information to be maintained in WM. To subtract superimposing waveforms elicited at the visual onset the stimuli to-be-remembered over motor cortices, we imported individual markers from the participants' motor responses in trials of the visual-motor condition to the corresponding segments of the visual-only condition. By doing this we created 'virtual markers' in the visual-only condition at the same timing in which a motor response in the visual-motor task was executed. Then, activity from visual-only trials locked to this virtual response was subtracted to the mean amplitudes of the visual-motor trials (containing both motor and visual evoked potentials). This process provided us with MCPs from which visual activity spreading from more posterior areas was subtracted (Figure 1B). This methodology is based on previous studies examining integration and dissociation of brain activity from distinct modalities (Galvez-Pol et al., 2018; Sel et al., 2014; Senkowski et al., 2007; Talsma et al., 2010; Talsma and Woldorff, 2005), as well as a more recent study examining motor activity linked to decision making and volitional processing of movement (Alexander et al., 2016).

Last, in all analyses, Mauchly's W was computed to check for violations of the sphericity assumption and Greenhouse–Geisser adjustments to the degrees of freedom were applied when appropriate. The P values were corrected for multiple comparisons using Bonferroni correction. Specifically, to account for multiple comparisons in the further analyses of memory load across ROIs in the MCPs, the significance level was Bonferroni-corrected (corrected *P* values: 0.05/2).

2.4.3. Electrophysiological source localization

Based on the scalp-recorded electric potential distribution, the Standardised Low Resolution Brain Electromagnetic Tomography (s-LORETA; Pascual-Marqui et al., 1994; Pascual-Marqui, 2002) was used to estimate the brain generators associated with modulations by memory load between stimuli types in MCPs. Specifically, the differential activity between the hand and shape stimuli conditions in the time window from -500 to -50ms of the MCPs after subtraction of visual-only trials' activity was subjected to source localization. sLORETA provides an approximate three-dimensional discrete solution to the inverse EEG problem. It estimates the most active brain areas using a 5mm resolution brain volume template of the Montreal Neurological Institute (MNI). MNI coordinates were translated to Talairach coordinates by Talairach Daemon. Compared with other dipole-based methods, s-LORETA has the advantage of estimating activity sources without any a priori assumptions about the number of sources or their location.

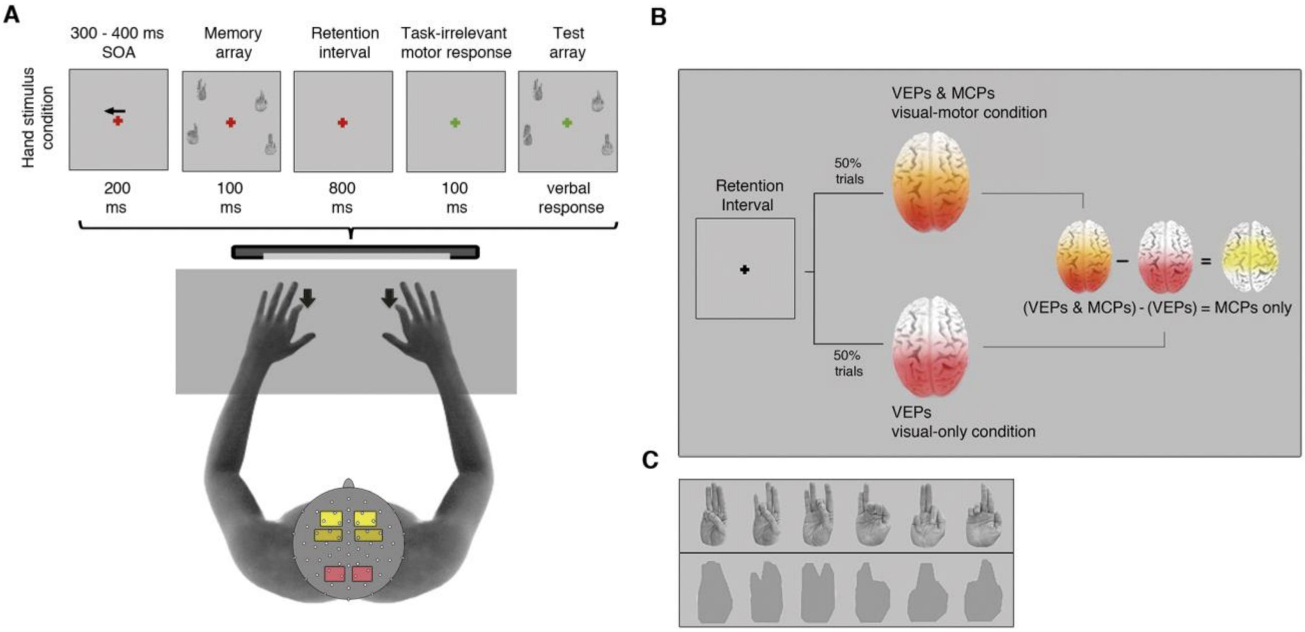

Figure 1 Task design, schematic illustration of subtractive methodology, and example of stimuli. *(A)* All participants performed a visual WM task for body-related images (hands) and control non-body-related images (shapes) in counterbalanced order. Participants verbally responded whether or not the stimuli in the left or right hemifield (as indicated by the central black arrow) were the same in the memory and test arrays. In half of the trials, participants performed a task-irrelevant motor response by simultaneously pressing two different keys with both index fingertips at the onset of the green fixation cross array. Electrode map highlights electrodes over visual (red) and motor ROIs (light and dark yellow) included in statistical analyses. SOA: stimulus onset asynchrony. *(B)* Schema of the subtraction methodology employed to isolate MCPs from concomitant visual processing of the images. The visual-motor condition (50% of trials) included visual-evoked potentials (VEPs) elicited at the onset of the visual array and MCPs elicited by the participants' task-irrelevant key pressing at the end of the retention interval (central-upper section). The visual-only condition consisted of only VEPs (central-bottom section) elicited at the onset of the visual array. The subtraction illustrated on the right [visual-motor condition]-[visual-only condition] allows isolating motor processing as indexed by MCPs free of concurrent visual activity. *(C)*

Example of 6 grey scaled right hands depicting different hand/finger positions and control shapes stimuli.

3. Results

3.1. Behavioural results

In the shape stimulus condition, participants correctly reported differences or similarities between the memory and test array in 78% of all trials in the visual-only condition and in 73.5% of all trials in the visual-motor. Very similar performance was present in the hand stimulus condition with 77% of all trials in the visual-only and in 73% of all trials in the visual-motor condition. Performance was analysed using the sensitivity index *d*', which considers false alarms and hit rates, representing a more precise measurement of signal detection than percentage of correct trials only. Repeated measures ANOVA with factors stimulus type (shapes versus hands), task (visual-only versus visual-motor), and memory load (1 versus 2) showed main effects of task ($F_{(1,19)} = 52.127$, $p < 0.001$, $\eta_p^2 = 0.732$) and load ($F_{(1,19)} = 238.249$, $p < 0.001$, $\eta_p^2 = 0.926$), as well as a significant interaction of stimulus type and load ($F_{(1,19)} = 6.718$, $p = 0.018$, $\eta_p^2 = 0.261$). We followed up this stimulus type X load interaction by separately comparing across the stimuli for load 1 and load 2 (i.e., shapes load 1 *vs.* hands load 1; shapes load 2 *vs.* hands load 2). No significant differences between stimulus type were found for either memory load ($t_{(1,19)} = 1.105$, $p = 0.283$, $d = 0.247$ and $t_{(1,19)} = -1.554$, $p = 0.137$, $d = -0.347$; respectively). We also compared separately the effect of memory load within each stimulus type (i.e., shapes load 1 *vs.* load 2; hands load 1 *vs.* load 2). The analyses yielded significant differences in both the shape ($t_{(1,19)} = 11.300$, $p < 0.0001$, $d = 2.526$) and hand stimulus type ($t_{(1,19)} = 16.302$, $p < p < 0.0001$, $d = 3.645$). No significant interaction of stimulus type X task X load was found ($F_{(1,19)} = 0.236$, $p = 0.633$, $\eta_p^2 = 0.012$). We also examined the reaction time for the bi-manual task-irrelevant motor response, which was measured from the onset of the colour change in the fixation cross. On average, participants responded after 253.5ms in the shape stimulus condition and 254ms in the hand condition. Participants consistently took slightly longer to exert the motor response when holding in memory two compared to one stimulus ($F_{(1,19)} = 19.538$, $p < 0.001$, $\eta_p^2 = 0.507$). Importantly, no main effect of stimulus type and no interaction between stimulus and memory load were found ($F_{(1,19)} = 0.009$, $p = 0.926$, $\eta_p^2 = 0.0005$; $F_{(1,19)} = 0.835$, $p = 0.372$, $\eta_p^2 = 0.042$, respectively). Overall, we intended to examine distinctive modulation of motor activity due to the type of information embedded in the visual stimuli (body *vs.* non-body-related) and not because of differences in the effect of the task-irrelevant motor responses across our stimulus conditions. The results obtained in the analyses of the sensitivity index *d'* were similar in the shape and hand stimulus conditions and the task-irrelevant motor responses did not modulate differentially the performance across these stimulus conditions (Figure 2).

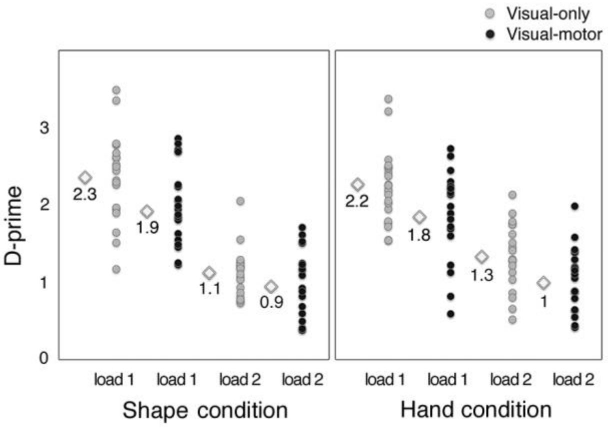

Figure 2 Behavioural results in visual and visual-motor conditions. Dots are the individual participants' d'prime means; the diamond shapes the sample average. Performance in hand and shape conditions matched as no significant interactions were found between performance for memory load 1 and 2 in the hand and shape conditions (all $Ps \geq 0.05$), n=20. D-prime: sensitivity index, $d' = Z$ (hit rate) – Z (false alarm rate).

3.2. Visual encoding of images: visual evoked potentials from visual-only trials (locked to visual memory array)

Visual evoked-potentials elicited at parietal and occipital electrode sites contralateral and ipsilateral to the cued hemifield were analysed for both memory loads and stimulus conditions. Approximately 300ms after the onset of the visual arrays, a contralateral persistent negativity appeared for the shape and hand stimuli conditions (Figure 3). This visual contralateral delayed activity (vCDA) continued across the retention interval and increased with the number of images to-be-remembered. We examined this activity across memory loads by subtracting waveforms elicited in the ipsilateral hemisphere to the waveforms elicited in the contralateral hemisphere to the cued hemifield. This latter step is assumed to remove nonspecific bilateral contributions of brain activity (Luck, 2012). We then computed repeated-measures ANOVA for each stimuli type with hemisphere (contralateral *vs.* ipsilateral) and memory load (1 *vs.* 2) as factors. In the shape stimulus condition, the interaction hemisphere by load yielded a significant main effect of memory load ($F_{(1,19)} = 9.101$, $p = 0.007$, $\eta_p^2 = 0.323$), hemisphere ($F_{(1,19)} = 21.679$, $p < 0.001$, $\eta_p^2 = 0.532$), as well as a significant interaction between load and hemisphere ($\mathrm{F}_{(1,19)} = 6.742$, $p = 0.018$, $\eta_p^2 = 0.261$). We followed up this interhemispheric difference by comparing mean amplitudes separately within hemispheres for load 1 and 2. In the subsequent analyses we compared mean amplitudes from the ipsilateral cortex when maintaining 1 and 2 items in WM ($t_{(19)} = 2.149$, $p = 0.045$, $d = 0.480$) and the contralateral hemisphere ($t_{(19)} = 3.425$, $p = 0.003$, $d = 0.765$). For the hand stimulus condition, significant main effects of load ($F_{(1,19)} = 9.899$, $p = 0.005$, $\eta_p^2 = 0.342$) and hemisphere ($F_{(1,19)} = 26.815$, $p < 0.001$, $\eta_p^2 = 0.585$), as well as a significant interaction between load and hemisphere ($F_{(1,19)} = 11.552$, $p = 0.003$, $\eta_p^2 = 0.378$) were found (Figure 3A). Follow up analyses separated for each hemisphere showed no differences of mean amplitudes over the ipsilateral hemisphere ($t_{(19)} = 1.783$, $p = 0.091$, $d = 0.398$). Conversely, in the contralateral hemisphere we found a significant difference between holding 1 or 2 stimuli in WM ($t_{(19)} = 3.818$, $p = 0.001$, $d = 0.853$). Taken together, the vCDA, a neural marker indexing maintenance of information in visual WM (Luck and Vogel, 2013) was present for both stimulus types.

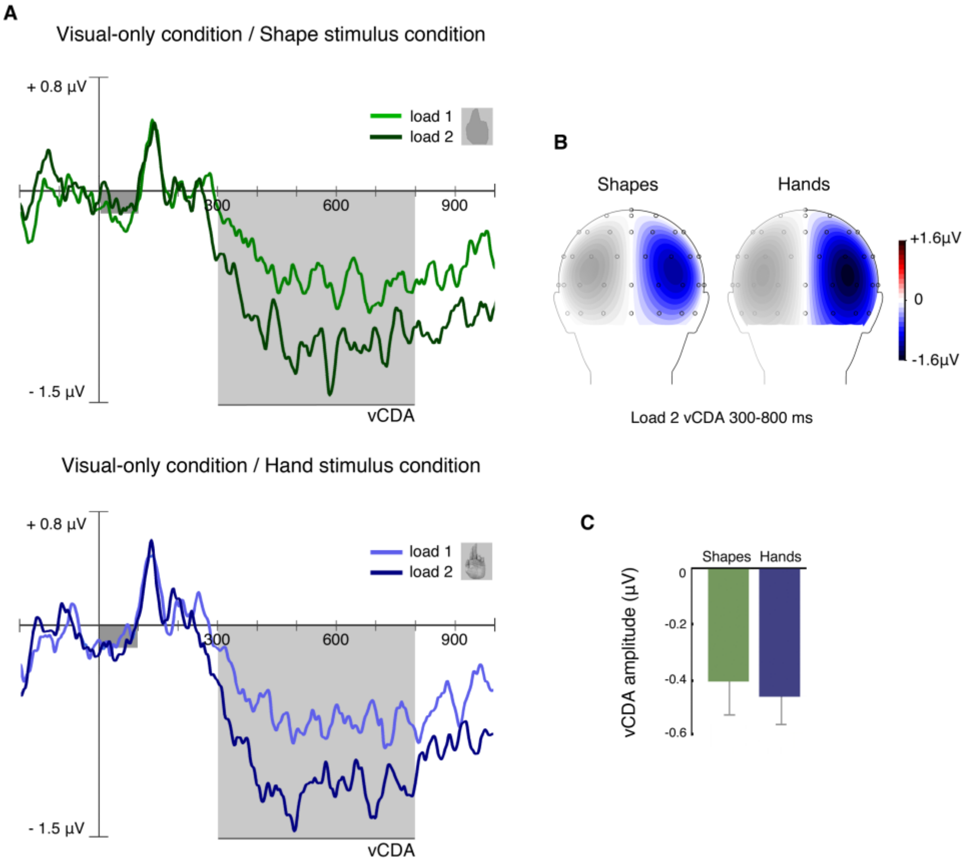

Figure 3 *Visual encoding of images:* Results of visual potentials locked to the memory array. *(A)* Contralateral minus ipsilateral visual-evoked potentials pooled over lateral occipital and posterior parietal electrodes (midway between POz and PO3, PO7 and P3; POz and PO4, PO8 and P4; visual ROI in figure 1A) for each memory load and stimulus type. Analysis of variance yielded a significant difference between memory loads 1 and 2 in both stimuli types. Large grey squares indicate time windows for statistical analyses*;* vCDA: visual contralateral delay activity. *(B)* Topography of the vCDA after onset of the memory array in load 2, showing an occipital-parietal peak in the time window 300-800ms. Topographical maps show contralateral minus ipsilateral amplitude differences projected on the right hemisphere. *(C)* Differential activity between contralateral minus ipsilateral activity in load 2 minus load 1 for both stimuli conditions. Error bars represent within subject SEMs; n=20. Notwithstanding

differences in the appearance of our stimulus conditions, we expected fairly similar visual processing in our visual WM task. In the analyses of VEPs,Here we also analysed the interaction of hemisphere by memory load individually in each stimulus condition to examine how the different waveforms develop along the time course. However, the triple interaction between stimulus, hemisphere, and load does did not reach significance (p = 0.257).

3.3. Motor encoding of images: Motor cortical potentials from visual-motor trials (locked to motor response)

To examine brain activity from neural responses within motor regions in this visual WM task, over and above concomitant visual activity leaking from posterior to more frontal areas of the brain comprising motor regions, we subtracted mean amplitudes of visually elicited activity (visual-only trials) from mean amplitudes including both visual and motorically elicited cortical potentials during the same experimental session (visual-motor trials) (Figure 4B). If sensorimotor areas were involved in both perceptual and mnemonic processing, motor-related cortices, known to participate in perception and representation of bodily information, would reflect differences of mean amplitudes modulated by the quantity of body-related information to be maintained in WM (i.e., effects of memory load in the hand stimulus condition).

MCPs in form of sharp preceding motor activity were clearly visible over frontocentral and frontal regions in both stimuli conditions. We computed mean amplitudes after deduction of visual activity elicited in visual-only trials to the visual-motor trials in the time window from -500 to -50ms (0ms: participants' motor response). MCPs elicited over contralateral and ipsilateral to the cued hemifield were analysed for both memory loads and stimulus conditions across frontocentral (C1 and FC1/midway between C1 and FC2, FC3/FC4, FC5/FC6) and frontal ROIs (F1/F2, F5/F6, and AF3/AF4 of the 10/20 system) (Kranczioch et al., 2009; Smith and Staines, 2012; Smulders and Miller, 2012). Specifically, repeated measures ANOVA with hemisphere (contralateral, ipsilateral), memory load (1,2), stimulus type (hand, shapes), ROIs (frontocentral, frontal), and electrode (3 electrodes) yielded main effects of ROI ($F_{(1,19)} = 32.251$, $p < 0.001$, $\eta_p^2 = 0.629$) and electrode ($F_{(2,38)} = 10.149$, $p = 0.002$, $\eta_p^2 = 0.348$), significant double interactions between stimulus type and hemisphere ($F_{(1,19)} = 4.931$, $p = 0.039$, $\eta_p^2 = 0.206$), hemisphere and electrode ($F_{(2,38)} = 4.979$, $p = 0.012$, $\eta_p^2 = 0.207$), load and ROI ($F_{(1,19)} = 8.906$, $p = 0.008$, $\eta_p^2 = 0.319$), and significant triple interactions between load, hemisphere, and ROI ($\mathrm{F}_{(1,19)} = 6.769$, $p = 0.018$, $\eta_p^2 = 0.262$) and stimulus type, hemisphere, and electrode ($F_{(2,38)} = 4.630$, $p = 0.027$, $\eta_p^2 = 0.195$). Crucially, we also found a significant interaction between all factors ($F_{(2,38)} = 5.995$, $p = 0.005$, $\eta_p^2 = 0.239$). We followed up this latter interaction separately for each hemisphere. In the ipsilateral hemisphere we found main effects of ROI ($F_{(1,19)} = 28.962$, $p < 0.001$, $\eta_p^2 = 0.603$) and electrode ($F_{(2,38)} = 9.122$, $p = 0.003$, $\eta_p^2 = 0.324$). The factor stimulus approached significance ($F_{(1,19)} = 3.362$, $p = 0.082$, $\eta_p^2 = 0.150$). No other significant effects and interactions were found (all *ps* > 0.05). In the contralateral hemisphere, we found main effects of ROI ($F_{(1,19)} = 34.451$, $p < 0.001$, $\eta_p^2 = 0.644$) and electrode ($F_{(2,38)} = 11.392$, $p < 0.001$, $\eta_p^2 = 0.374$). Interestingly, the results showed a marginal interaction between stimulus type and ROI ($F_{(1,19)} = 4.209$, $p = 0.054$, $\eta_p^2 = 0.181$), which reached significance in interaction with load: stimulus type x ROI x load ($F_{(1,19)} = 6.046$, $p = 0.024$, $\eta_p^2 = 0.241$).

Given this interaction over the contralateral hemisphere between stimuli types, ROI and load, we proceed to examine the modulation of memory load by ROI for each stimulus condition. For shape stimuli, no main effect of load ($F_{(1,19)} = 0.093$, $p = 0.763$, $\eta_p^2 = 0.004$) or interaction between load and ROI ($F_{(1,19)} = 0.162$, $p = 0.692$, $\eta_p^2 = 0.008$) were found. The results only showed a main effect of ROI ($F_{(1,19)} = 58.942$, $p < 0.001$, $\eta_p^2 = 0.756$), indicating a significant difference between the frontocentral and more frontal ROI regardless of memory load ($t_{(1,19)} = 7.678$, $p < 0.001$, $d = 1.716$). Contrary, maintaining hand images in WM elicited mean amplitudes that were distinctively modulated across ROIs ($F_{(1,19)} = 13.573$, $p < 0.002$, $\eta_p^2 = 0.416$) depending on the number of hand images (i.e. hands) to be remembered ($F_{(1,19)} = 20.811$, $p < 0.001$, $\eta_p^2 = 0.522$). Follow up of analyses separated by ROIs showed a significant difference of mean amplitudes in the frontal ROI when holding one hand *vs.* two hands ($t_{(1,19)}$ = 3.260, p = 0.004, d = 0.743; in contrast, frontocentral ROI ($t_{(1,19)}$ = -.676, p = 0.507, d = -0.151) (Figure 4A).

In addition, we also computed the interaction between hemisphere and memory load over the same posterior electrodes used in the analysis of stimulus-locked potentials from visual-only trials (i.e., vCDA). After subtraction of visual-evoked potentials, for both stimulus conditions repeated-measures ANOVA yielded no significant main effects of hemisphere or load (all $ps > 0.05$). Moreover, the interaction between these factors did not reach significance when memorising geometrical shapes ($F_{(1,19)}$ = 0.175, p = 0.680, η_p^2 = 0.009) or hand stimuli ($F_{(1,19)}$ = 0.076 p = 0.786, η_p^2 = 0.004). These latter results confirm that visual activity was certainly subtracted from the concurrent visual and motor activity of the visual-motor trials.

Taken together, MCPs modulated by memory load were found in the hand stimulus condition whereas no modulation by load was found in the shape stimulus condition. Importantly, mean amplitudes over frontal electrode sites of the hemisphere contralateral to the hand stimuli to-be-remembered showed a significant difference between maintaining in 1 or 2 hand images in WM. Our results suggest that maintaining in WM body-related stimuli such as hand images involves neural recruitment of motor regions, which are known to underpin the perceptual representation of body stimuli beyond visual cortices (i.e., involvement of sensorimotor cortex in WM for visually perceived body-related information).

3.4. Electrophysiological source localization

Based on the scalp-recorded electric potential distribution, the Standardised Low-Resolution Brain Electromagnetic Tomography (sLORETA) (Pascual-Marqui, 2002) was used to estimate cortical source estimation. It was performed on the MCPs (response-locked potentials, -500 to -50ms) after subtraction of visual-evoked potentials from visual-only trials, as well as after obtaining the differential brain activity between stimuli types once subtracted memory loads (i.e., load 2 minus load 1 for each stimulus type). This identified a set of candidate regions where maximum differential activity was due to load differences between stimuli conditions including classic motor cortical regions, in precentral and superior frontal gyrus (Brodmann areas 6/4), and postcentral gyrus over parietal lobe (BA 3). These comprise premotor cortex, SMA, primary motor cortex, and primary somatosensory cortex over caudal postcentral regions (Figure 4D).

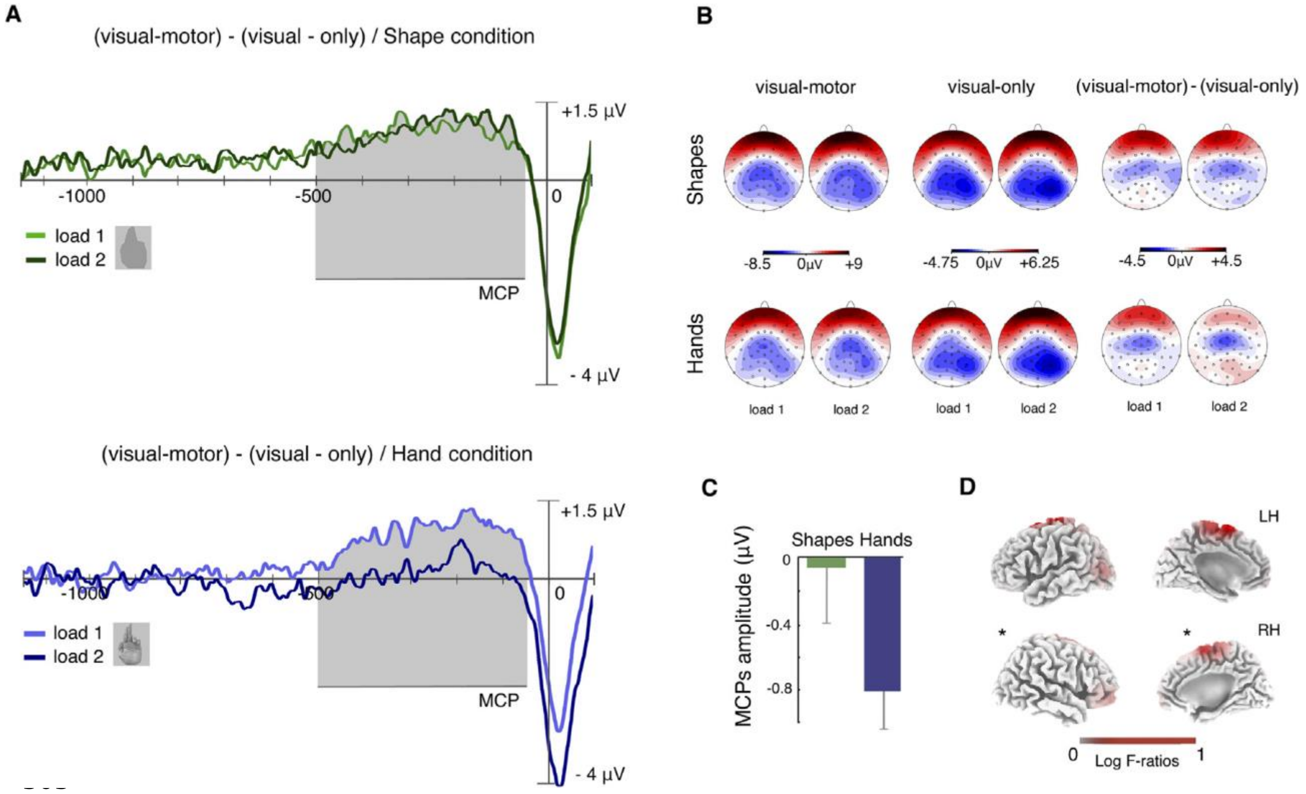

Figure 4 *Motor encoding of images:* Results of finger response-locked motor-cortical potentials (MCPs). *(A)* Contralateral waveforms pooled over frontal electrodes (F1/F2, F5/F6, and AF3/AF4; frontal ROI in figure 1A) for each memory load and stimulus conditions after subtracting activity from the visual-only trials to the visual-motor trials. Motor preceding activity can be observed nearly half second before the actual motor response (0ms). A significant difference of mean amplitudes modulated by memory load was only found in the hand stimulus condition. No differences were found in the shape stimulus condition. *(B)* Whole topographical maps in all conditions, including task, memory load, stimulus conditions, and the subtraction of visual only trials' activity to visual-motor trials' activity (-500 to -50ms). *(C)* Differential activity between load 2 and load 1 for both stimuli conditions.

Error bars represent SEMs. *(D)* Three-dimensional representation of sLORETA showing candidate regions with maximal differences due to load differences (i.e., load 2 minus load 1) between stimuli conditions. Grey squares indicate time windows for statistical analyses and sLORETA; n=20.

3.5. Signal-to-noise ratio.

Given the subtractive nature of our methodology, it is possible that variance in the signal-to-noise ratio in the subsequent conditions could bias our analyses and results between stimuli types. To rule out this possibility, we also examined the number of accepted trials separately for trials cued to left and right hemifield, for each memory load and type of stimulus in the *visual-motor* and *visual-only* conditions. The only significant results were found as main effects of task (visual-only, visual-motor) ($F_{(1,19)} = 5.695$, $p = 0.028$, $\eta_p^2 = 0.230$) and load (1,2) ($F_{(1,19)} = 123.394$, $p < 0.001$, $\eta_p^2 = 0.866$). No main effects of cue ($F_{(1,19)} = 0.780$, $P = 0.388$, $\eta_p^2 = 0.019$), stimulus conditions ($F_{(1,19)} = 0.633$, $p = 0.436$, $\eta_p^2 = 0.032$), nor significant interaction between all factors was found (all *ps* > 0.067). These results denote that signal-to-noise ratio did not bias the results on later subtractions across stimuli conditions. The dissimilarities of mean amplitudes over sensorimotor regions sites would be likely due to effects of memory load when processing visual information conveying distinctive properties (body and non-body-related).

4. Discussion

In the current study we examined the neural recruitment of visual and sensorimotor brain areas in a WM task where the stimuli to-be-remembered were body and non-body-related stimuli. We developed a novel paradigm combining findings in WM, action perception, and embodiment. Namely, sensory recruitment models of WM, which postulate that brain areas with a role in the perception of the stimuli are also involved during the consolidation of these in WM (D'Esposito and Postle, 2015; Postle, 2006; Serences et al., 2009), as well as embodiment and internal motor simulation approaches suggesting that visually perceiving bodily information engages one's body representation in sensorimotor cortex (Calvo-Merino et a., 2006; Urgesi et al., 2007). From these two approaches surges our hypothesis regarding the potential involvement of motor cortices during consolidation of body-related stimuli in visual WM. To test this, we integrated for the first time a classical index of motor activation (namely motor-cortical potentials, MCP), in a visual working memory task of body images. Specifically, we evoked visual and motor-cortical potentials in a delayed-match-to-sample paradigm where stimuli to-be-remembered were images conveying different degrees of sensorimotor information (body and non-body-related images; hand *vs.* shape).

Our results show that persistent activity resulting from visual evoked-potentials locked to the onset of the visual array containing stimuli to-be-remembered increased in the contralateral visual cortex. Previous studies using arbitrary stimuli similar to our control stimulus condition have also shown similar activity over posterior parietal and occipital electrode sites (McCollough et al., 2007; Todd and Marois, 2004; Tsubomi et al., 2013). This form of persistent activity is generally interpreted as a neural marker of attention-based rehearsal of visual information.

Importantly, motor activity was examined via MCPs that were elicited through a self-initiated bimanual key pressing task that was irrelevant for the mnemonic task and executed during the active maintenance of the visual images in WM. This manipulation elicited a motor neural signature (namely MCPs) over frontal electrode sites in both hemispheres for both stimulus conditions. Subsequent analyses revealed that only the hemisphere contralateral to the encoded hemispace exhibited a modulation of mean amplitude by memory load and stimulus type. Remarkably, only in the hand stimulus condition the modulation of MCPs by memory load was present; this involves the interaction of a neural signature source localised in motor brain areas (Ikeda et al., 1992; Lu et al., 2012; Shibasaki and Hallett, 2006; Yazawa et al., 2000) with memory load conveyed in the visual stimuli. This latter finding goes beyond classical accounts of embodiment that stress the importance of our own body and motor representations in the perception of body-related information (Calvo-Merino et al., 2006; De Vignemont, 2011), and provides evidence of the engagement of motor cortices during the encoding and maintenance of body-related information in a visual WM task.

4.1. Recruitment of motor cortex in a visual working memory task of body-related information

Premotor cortex, SMA, and the primary motor cortex have been linked to the perception of body-related information (e.g., kinematics, biological motion, body images), as well as sensory guidance of movement and control of the body, sequencing, planning, initiating, learning, and imagining movements. Evidence for this comes from electrophysiological studies reporting modulation of MCPs over sensorimotor brain regions when observing other's actions (Holländer et al., 2011; Kilner et al., 2004; van Schie et al., 2004) and when preparing or imagining hand actions with different level of motor complexity (Kranczioch et al., 2010, 2009). Likewise, neuroimaging studies have shown long lasting effects of body experience (i.e., a form of motor long-term memory) in sensorimotor cortex during action observation (Calvo-Merino et al., 2006, 2005; Orgs et al., 2008), as well as modulation of activity in motor cortex related to the affordability of the objects to be maintained in WM (Mecklinger et al., 2004, 2002). Here, we provide new evidence supporting the involvement of motor cortex in visual high-order cognitive processes beyond perception. Importantly, the combination of visual and motor evoked responses within the same trial and the isolation of superimposed neural components (Galvez-Pol et al., 2018; Sel et al., 2014; Talsma and Woldorff, 2005) provides this motor response a significant role in visual working memory over and above potential carry over effects from visual processing.

Our results are consistent with earlier work in visual WM suggesting how neural recruitment across cortical regions depends on the stimuli's features to-be-remembered (Gazzaley et al., 2004; Lee et al., 2013; Serences et al., 2009). Here we compared body-related visual information with analogous non-body-related information (hand vs. shape conditions). While both stimulus conditions show similar behavioural performance and engagement in visual sensory cortices, we find differences between the hand and shape conditions in the modulation of the motor cortical responses. We attribute this MCP differences to recruitment of sensory associations related to the memoranda rather than to a mere effect of complexity during early visual processing (Brady et al., 2016; Galvez-Pol et al., 2018; Konkle and Brady, 2010; McWeeny et al., 1987).

4.2. Present challenges and forthcoming questions

Our results show modulation of visual-evoked potentials for the two stimulus conditions, but only WM maintenance of body-related images modulates MCPs. One interesting question arises from the relationship between this specific modulation and its relationship with the mnemonic content of the perceived stimuli. Previous behavioural studies reported that WM maintenance of visually perceived actions is impaired when a concurrent body-related task is performed. Interestingly, this effect has been observed whether the actions need to be reproduced (Smyth et al., 1988; Smyth and Pendleton, 1989) or visually recognized in a delayed-match paradigm (Moreau, 2013; Wood, 2007). Moreover, WM for body-related information is also impaired by secondary task that involve active maintenance, as well as mere perception of additional body stimuli (Smyth and Pendleton, 1990). More recent studies highlight content-specific processing across both visual and motor cortices. Two cortical pathways have been identified in the processing of identity and motion information in occipitotemporal regions (extrastriate body area, EBA) and premotor cortices (Urgesi et al., 2007). On a similar note, Wurm and Lingnau (2015) showed that during action observation brain activity in inferior parietal and occipitotemporal cortex can be decoded for the abstract levels of the observed actions whereas activity in the premotor cortex can be decoded for their concrete levels (i.e., specific kinematics). Our results provide a stepping-stone to studies investigating the specific features of the body stimuli that motor cortices encode and maintain in visual working memory.

4.3. Conclusion

By measuring visual-evoked potentials and MCPs in a visual WM task for body and non-body-related stimuli, we found distinct neural responses across visual and motor brain areas. Visual brain areas were modulated by memory load in both stimulus conditions whereas sensorimotor regions over frontal cortices were only modulated when maintaining in memory body-related stimuli (i.e., hand images). Importantly, this later motor activation was significant over and above carry over effects from visual neural responses. Previous studies have shown that visual information elicits modulation by memory load in posterior and visual cortices (McCollough et al., 2007; Todd and Marois, 2004; Tsubomi et al., 2013; Vogel and Machizawa, 2004) and tactile information in somatosensory cortices (Harris et al., 2002; Katus and Eimer, 2016). The results of the present study suggest a more dynamic process beyond the classical early sensory processing, in which the nature of the information embedded in the memoranda seems to elicit prior sensorimotor associations. Overall, our findings suggest motor resonance by means of memory load in functionally different cortical regions that match the characteristics of the perceived stimuli. This is consistent with a memory framework in which the nature of the information embedded in the visual memoranda drives its further neural handling.

Author contributions

A.G-P, B.C.-M, and B.F designed the research; A.G-P collected the data; A.G-P, B.C.-M, and B.F. analysed and interpreted the data; A.G-P and B.C.-M wrote drafts of the manuscript, and B.F provided critical comments on the paper.

Ethics

Human subjects: Ethical approval for methods and procedures was obtained from the City, University of London Psychology Department's Research Ethics Committee. All participants provided written, informed consent.

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The authors declare no conflict of interest.

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