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

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26 **Abstract**

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

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

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52 **Highlights**

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

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75 **1. Introduction**

76 Perceiving and reflecting about others is a crucial aspect of human cognition. On the
77 one hand, perceiving actions, body-tool interactions, and images of body parts engages our
78 own body representations in somatosensory and sensorimotor regions, over and above visual
79 brain areas (Caspers et al., 2010; Molenberghs et al., 2012). These findings have been
80 conceptualised within the embodiment framework, suggesting that the aforementioned
81 activations reflect our ability to process bodily percepts and other stimuli at the sensory,
82 motor, and/or affective levels in the same ways as one's own body (Calvo-Merino et al.,
83 2005; De Vignemont, 2011; Gallese and Sinigaglia, 2011; Sel et al., 2014; Urgesi et al.,
84 2007). On the other hand, reflecting about others also entails the temporary retention of body-
85 related information beyond its immediate physical presence (beyond perception), a process
86 known as working memory (WM). Interestingly, the results of a recent electrophysiological
87 study (Galvez-Pol et al., 2018) suggest the involvement of somatosensory regions, which are
88 highly interconnected with further sensorimotor cortices, during WM for visually perceived
89 body-related information. Also, earlier behavioural studies indicate the contribution of
90 sensorimotor regions during the encoding and consolidation of visually perceived bodily
91 information in WM (Shen et al., 2014; Smyth et al., 1988; Smyth and Pendleton, 1989;
92 Wood, 2007), however the concomitant neural underpinnings of this phenomenon are unclear.

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

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

105 In the present study we used a stimulus set involving images of hands depicting
106 different postures. For the control non-body-related stimuli, we developed an additional set of
107 polygonal shapes based on the outline of the hands. We matched the discriminability between
108 stimulus conditions in earlier pilot experiments and also report similar discriminability
109 between these stimuli in our latest work in WM (Galvez-Pol et al., 2018). We expect that
110 notwithstanding differences in the appearance of the stimuli (body and non-body-related),
111 memory processing and recorded activity may be driven by conceptual rather than perceptual
112 complexity; which is congruent with previous memory studies (Konkle and Brady 2010;
113 McWeeny et al. 1987; Brady et al., 2016). Secondly, we developed a novel paradigm that
114 enables investigating activity in visual cortex and motor regions by dissociating sensorimotor
115 activity from concomitant activity due to the visual processing of body-related images in a
116 visual WM task (as opposed to encoding WM maintenance of non-body-related images). This
117 paradigm takes advantage of the lateralized organization of the visual and motor system and
118 two well-known electroencephalographic components indexing visual and motor processing.
119 The first component is the visual contralateral delay activity (vCDA), which refers to a
120 visual-evoked potential in the form of persistent activity that increases with the number of
121 stimuli to-be-remembered in the posterior-contralateral hemisphere to the encoded visual field
122 (Luria et al., 2016; Vogel and Machizawa, 2004). The second component is a motor-cortical
123 potential (MCP) resembling that observed before self-initiated movements in the readiness
124 potential, also known as *Bereitschaftspotential* (Deecke et al., 1976; Smulders and Miller,
125 2012); a component arising from motor and premotor cortices and known to reflect the
126 underlying processing of one's motor responses, such as the forthcoming complexity of an
127 executed or imagined action (Kranzloch et al., 2010, 2009), as well as others' observed
128 bodily actions (van Schie et al., 2004).

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

144

145 **2. Materials and Methods**

146 *2.1. Participants*

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

152 *2.2. Stimuli*

153 The stimuli presented in the current study were developed from a larger set of 27
154 pairs of hand images depicting different postures. The selection criterion was the following:

155 selecting images that did not convey meaning or symbolism (e.g., a fist with the thumb up
156 could be remembered as ‘OK’). Similarly, we wanted to avoid participants counting the
157 number of fingers up, therefore, to lessen this strategy all stimuli have 2 or 3 fingers up.
158 Finally, a set of 6 pictures of right hands depicting different hand postures and finger
159 positions with no meaning or symbolism was used (Figure 1C). These hands were
160 horizontally rotated to the left, obtaining 6 pairs of right and left hands that were then
161 greyscaled. We created a control condition composed by a set of geometrical shapes matching
162 the hands’ outline, size, and colour. We piloted these stimuli and made small adjustments to
163 obtain similar discriminability. Our recent work in WM using these stimuli reports similar
164 discriminability (Galvez-Pol et al., 2018)

165 2.3. *Experimental design and procedure*

166 Participants were seated in front of a LCD monitor (75 Hz) in a dimly lit,
167 electromagnetically shielded room. Participants’ forearms rested on the top of a table with
168 their hands separated about 25cm, in palm down position, and covered by a black surface.
169 Participants performed both stimulus conditions (i.e., hands and geometrical shapes) in
170 counterbalanced order. They were instructed to judge differences between pairs of arrays
171 depicting different hand postures or shape forms. At the beginning of each trial a central
172 arrow cue (200ms) instructed the participants to covertly attend to the items in either the left
173 or the right hemifield. After the offset of the arrow cue (300-400ms), the memory array was
174 displayed for 100ms and followed by a blank retention interval (800ms). At the end of the
175 retention interval the fixation cross changed from red to green until the end of the trial, 100ms
176 after this colour change the test array was displayed. In the blocks with visual-only trials,
177 participants were instructed to ignore this colour change. In the blocks with visual-motor
178 trials, participants were instructed to prepare a task-irrelevant motor response during the
179 retention interval that had to be executed at the onset of the green fixation cross. This
180 response was done by simultaneously pressing two different keys with the index fingers of
181 both hands. Finally, the test array was displayed until participants verbally responded whether

182 or not the stimuli in the cued hemifield of the test array were identical to the memory array
183 (Figure 1A). One of the items in the test array differed from the memory array in 50% of the
184 trials; the rest of the stimuli remained the same. All trials were separated by a 700ms blank
185 interval.

186 The shape and hand images were displayed using E-Prime Software (Psychology
187 Software Tools). All stimulus arrays were presented within two $6^\circ \times 8.5^\circ$ rectangular regions
188 that were centred 4° to the left and right of a central fixation cross on a light grey background.
189 Each memory array consisted of 1 or 2 hands ($1.4^\circ \times 0.9^\circ$) in each hemifield, each stimulus
190 being randomly selected from the set of twelve hands. Right hands were shown on the right
191 hemifield while left hands were displayed on the left. The rationale behind this latter choice is
192 based on the clear contralateral representation of the hands in the motor cortex. This allows
193 observing contralateral activity over motor regions that can be dissociated from concomitant
194 visually evoked activity when seeing and remembering the stimuli. In the control condition 1
195 or 2 polygonal shapes ($1.4^\circ \times 0.9^\circ$) were selected and shown in a similar fashion. The
196 positions of all stimuli were randomized on each trial with the restriction that the distance
197 between stimuli within a hemifield was maintained to a minimum of 2.4° (centre to centre).
198 Since previous studies have shown that holding in WM two items may well lead to limits in
199 WM capacity (Alvarez and Cavanagh, 2004; Luria et al., 2010; Wood, 2007); memory load 1
200 and 2 would allow detecting increased activity related to memory encoding and maintenance
201 of the stimuli. Participants performed a total of 1344 trials, 672 for each stimulus condition
202 (hands and geometrical shapes). This is equal to 336 trials for each memory load condition
203 (load 1 and 2) of which half entailed the memory task irrelevant motor response (visual-motor
204 condition) and the other half visual only trials (visual-only condition). The following
205 experimental manipulations were randomly presented to the participants on trial by trial basis:
206 memory load, side of the cue, and location of the stimuli on the screen. The type of trials
207 (visual-motor and visual-only) were counterbalanced across blocks and the order of the
208 stimulus conditions was counterbalanced across participants.

209 2.4. EEG recording and data analysis.

210 Event-related potentials were recorded from 64 Ag/AgCL active electrodes mounted
211 equidistantly on an elastic electrode cap at standard locations of the international 10-10
212 system (M10 montage; EasyCap GmbH). Electrodes were referenced to the right mastoid and
213 re-referenced to the average reference off-line. Vertical and bipolar horizontal
214 electrooculogram was recorded for eye movements tracking and artifact correction purposes.
215 Continuous EEG was recorded using a BrainAmp amplifier (BrainProducts; 500 Hz sampling
216 rate). Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts).
217 The data were digitally low-pass-filtered at 30 Hz, and ocular correction was performed
218 (Gratton et al., 1983). Trials with horizontal eye movements (HEOG exceeding $\pm 55 \mu\text{V}$) or
219 other artifacts (voltage exceeding $\pm 85 \mu\text{V}$ at any electrode) were excluded from analyses.
220 The EEG signal was epoched into 1750ms segments, starting 200ms before the memory array
221 of each trial and ending 550ms after the offset of the green fixation cross. This included
222 activity associated with the visual processing of the memory array in the visual-only
223 condition (locked to the visual memory array), and activity associated with both the visual
224 processing of the memory array and the motor response that was elicited by the task irrelevant
225 key pressing in the visual-motor condition. All these segments were corrected relative to the
226 100 ms prestimulus interval. Following this, grand averages were computed based on correct
227 response trials. The corresponding segments locked to the visual memory array were epoched
228 into 1200ms and the segments comprising response-locked potentials were epoched into
229 1250ms (-1150ms preceding the motor response to 100ms after).

230 2.4.1. Visual-evoked potentials (locked to visual memory array)

231 Grand averages were computed independently for the two stimulus conditions,
232 separately for the two memory loads, and for visual-only trials by averaging brain waveforms
233 elicited at electrodes over the hemisphere contralateral and ipsilateral to the side to be
234 memorized as indicated by the central cue. Then, visual contralateral delay activity (vCDA)
235 was computed from 300 to 800ms after the onset of the visual memory array to-be-

236 remembered as the difference between contralateral amplitudes (averaging evoked potentials
237 over right visual hemisphere when attending left hemifield and over left visual hemisphere
238 when attending the right hemifield) and ipsilateral amplitudes (average of evoked potentials
239 over the right visual hemisphere when attending the right hemifield and *vice versa*) (Luck,
240 2012). Statistical analysis was performed for mean amplitudes in accordance with sites and
241 time windows reported in previous studies (Vogel et al., 2005; Vogel and Machizawa, 2004),
242 specifically, occipital and posterior parietal electrode sites (midway between POz and PO3,
243 midway between PO7 and P3 / midway between POz and PO4, midway between PO8 and P4
244 of the 10-20 system). To account for multiple comparisons in the further analyses of mean
245 amplitudes across hemispheres in the vCDA, the significance level was Bonferroni-corrected
246 (corrected *P* values: 0.05/2).

247 2.4.2. *Motor cortical potentials (locked to motor response - MCPs)*

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

255 MCPs were obtained by averaging the elicited activity preceding the task-irrelevant
256 motor response during the retention interval in the visual-motor condition, meaning that they
257 were measured with respect to the moment the participants performed the key pressing (from
258 -1150 to 100 ms, 0 ms being the actual key press). We then compute statistical analysis of
259 MCPs that allowed us to explore our main hypothesis: modulation of neural recruitment in
260 sensorimotor regions depending on the number of hand images to-be-remembered. In
261 accordance to the aforementioned temporal dynamics, as well as electrodes sites used in
262 previous research (Kranczioch et al., 2009; Smith and Staines, 2012; Smulders and Miller,

263 2012) we defined two regions of interested (ROIs) that were analysed from -500ms to -50ms
264 before the onset of the movement produced in the task-irrelevant motor response. There were
265 two (contralateral and ipsilateral) frontocentral (midway between C1 and FC1/midway
266 between C1 and FC2, FC3/FC4, FC5/FC6) and frontal ROIs (F1/F2, F5/F6, and AF3/AF4)
267 (Figure 1A). We averaged contralateral MCPs (averaging brain activity over right motor
268 hemisphere when attending left hemifield and over left motor hemisphere when attending the
269 right hemifield) and ipsilateral amplitudes (average of evoked potentials over the right
270 hemisphere when attending the right hemifield and *vice versa*). Factors included in the
271 analyses were hemisphere (contralateral, ipsilateral), ROI (frontocentral, frontal), electrode (3
272 levels), memory load (1,2), and stimulus condition (hand images, shape images).

273 2.4.2.1 Subtraction of evoked potentials

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

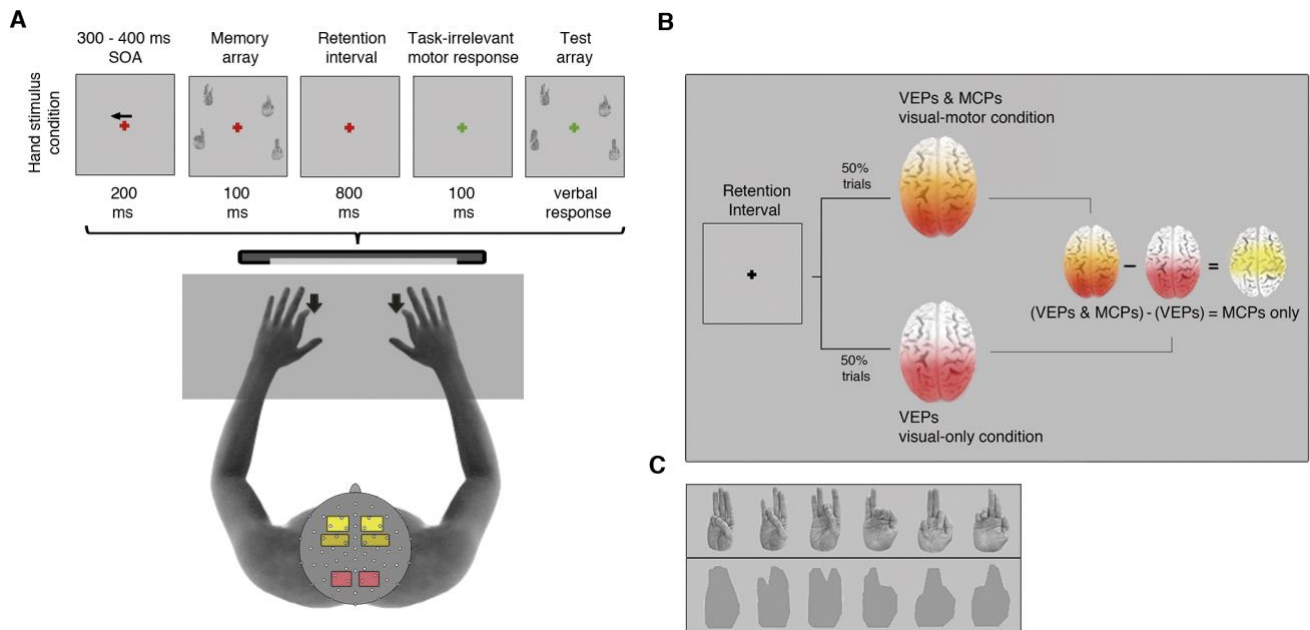
290 and Woldorff, 2005), as well as a more recent study examining motor activity linked to
291 decision making and volitional processing of movement (Alexander et al., 2016).

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

298 *2.4.3. Electrophysiological source localization*

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

311



313

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

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

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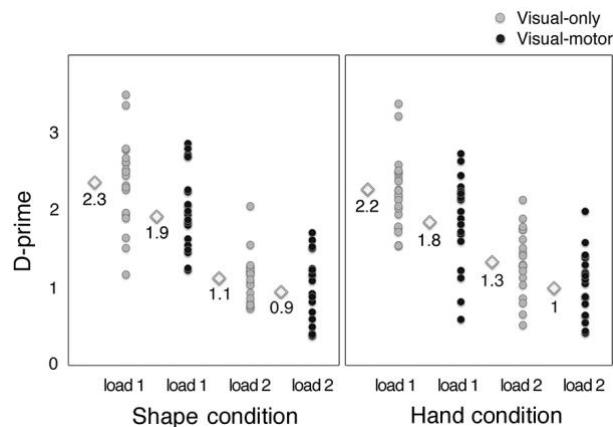
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334 **3. Results**

335 *3.1. Behavioural results*

336 In the shape stimulus condition, participants correctly reported differences or
337 similarities between the memory and test array in 78% of all trials in the visual-only condition
338 and in 73.5% of all trials in the visual-motor. Very similar performance was present in the
339 hand stimulus condition with 77% of all trials in the visual-only and in 73% of all trials in the
340 visual-motor condition. Performance was analysed using the sensitivity index d' , which
341 considers false alarms and hit rates, representing a more precise measurement of signal
342 detection than percentage of correct trials only. Repeated measures ANOVA with factors
343 stimulus type (shapes versus hands), task (visual-only versus visual-motor), and memory load
344 (1 versus 2) showed main effects of task ($F_{(1,19)} = 52.127, p < 0.001, \eta_p^2 = 0.732$) and load
345 ($F_{(1,19)} = 238.249, p < 0.001, \eta_p^2 = 0.926$), as well as a significant interaction of stimulus type
346 and load ($F_{(1,19)} = 6.718, p = 0.018, \eta_p^2 = 0.261$). We followed up this stimulus type X load
347 interaction by separately comparing across the stimuli for load 1 and load 2 (i.e., shapes load
348 1 vs. hands load 1; shapes load 2 vs. hands load 2). No significant differences between
349 stimulus type were found for either memory load ($t_{(1,19)} = 1.105, p = 0.283, d = 0.247$ and t
350 $_{(1,19)} = -1.554, p = 0.137, d = -0.347$; respectively). We also compared separately the effect of
351 memory load within each stimulus type (i.e., shapes load 1 vs. load 2; hands load 1 vs. load
352 2). The analyses yielded significant differences in both the shape ($t_{(1,19)} = 11.300, p < 0.0001,$
353 $d = 2.526$) and hand stimulus type ($t_{(1,19)} = 16.302, p < p < 0.0001, d = 3.645$). No significant
354 interaction of stimulus type X task X load was found ($F_{(1,19)} = 0.236, p = 0.633, \eta_p^2 = 0.012$).
355 We also examined the reaction time for the bi-manual task-irrelevant motor response, which

356 was measured from the onset of the colour change in the fixation cross. On average,
 357 participants responded after 253.5ms in the shape stimulus condition and 254ms in the hand
 358 condition. Participants consistently took slightly longer to exert the motor response when
 359 holding in memory two compared to one stimulus ($F_{(1,19)} = 19.538, p < 0.001, \eta_p^2 = 0.507$).
 360 Importantly, no main effect of stimulus type and no interaction between stimulus and memory
 361 load were found ($F_{(1,19)} = 0.009, p = 0.926, \eta_p^2 = 0.0005$; $F_{(1,19)} = 0.835, p = 0.372, \eta_p^2 =$
 362 0.042 , respectively). Overall, we intended to examine distinctive modulation of motor activity
 363 due to the type of information embedded in the visual stimuli (body vs. non-body-related) and
 364 not because of differences in the effect of the task-irrelevant motor responses across our
 365 stimulus conditions. The results obtained in the analyses of the sensitivity index d' were
 366 similar in the shape and hand stimulus conditions and the task-irrelevant motor responses did
 367 not modulate differentially the performance across these stimulus conditions (Figure 2).



368
 369 **Figure 2** Behavioural results in visual and visual-motor conditions. Dots are the individual
 370 participants' d' prime means; the diamond shapes the sample average. Performance in hand
 371 and shape conditions matched as no significant interactions were found between performance
 372 for memory load 1 and 2 in the hand and shape conditions (all $P_s \geq 0.05$), $n=20$. D-prime:
 373 sensitivity index, $d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$.

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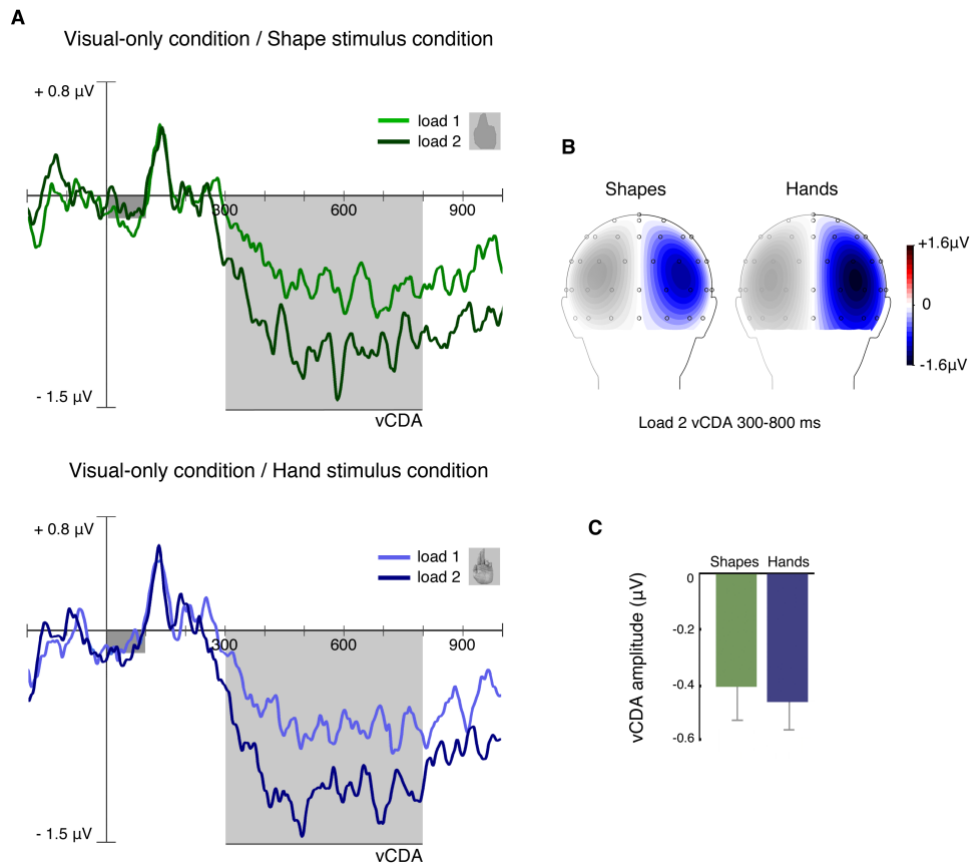
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377 3.2. Visual encoding of images: visual evoked potentials from visual-only trials (locked to
378 visual memory array)

379 Visual evoked-potentials elicited at parietal and occipital electrode sites contralateral
380 and ipsilateral to the cued hemifield were analysed for both memory loads and stimulus
381 conditions. Approximately 300ms after the onset of the visual arrays, a contralateral persistent
382 negativity appeared for the shape and hand stimuli conditions (Figure 3). This visual
383 contralateral delayed activity (vCDA) continued across the retention interval and increased
384 with the number of images to-be-remembered. We examined this activity across memory
385 loads by subtracting waveforms elicited in the ipsilateral hemisphere to the waveforms
386 elicited in the contralateral hemisphere to the cued hemifield. This latter step is assumed to
387 remove nonspecific bilateral contributions of brain activity (Luck, 2012). We then computed
388 repeated-measures ANOVA for each stimuli type with hemisphere (contralateral vs.
389 ipsilateral) and memory load (1 vs. 2) as factors. In the shape stimulus condition, the
390 interaction hemisphere by load yielded a significant main effect of memory load ($F_{(1,19)} =$
391 $9.101, p = 0.007, \eta_p^2 = 0.323$), hemisphere ($F_{(1,19)} = 21.679, p < 0.001, \eta_p^2 = 0.532$), as well as
392 a significant interaction between load and hemisphere ($F_{(1,19)} = 6.742, p = 0.018, \eta_p^2 = 0.261$).
393 We followed up this interhemispheric difference by comparing mean amplitudes separately
394 within hemispheres for load 1 and 2. In the subsequent analyses we compared mean
395 amplitudes from the ipsilateral cortex when maintaining 1 and 2 items in WM ($t_{(19)} = 2.149, p$
396 $= 0.045, d = 0.480$) and the contralateral hemisphere ($t_{(19)} = 3.425, p = 0.003, d = 0.765$). For
397 the hand stimulus condition, significant main effects of load ($F_{(1,19)} = 9.899, p = 0.005, \eta_p^2 =$
398 0.342) and hemisphere ($F_{(1,19)} = 26.815, p < 0.001, \eta_p^2 = 0.585$), as well as a significant
399 interaction between load and hemisphere ($F_{(1,19)} = 11.552, p = 0.003, \eta_p^2 = 0.378$) were found
400 (Figure 3A). Follow up analyses separated for each hemisphere showed no differences of
401 mean amplitudes over the ipsilateral hemisphere ($t_{(19)} = 1.783, p = 0.091, d = 0.398$).
402 Conversely, in the contralateral hemisphere we found a significant difference between
403 holding 1 or 2 stimuli in WM ($t_{(19)} = 3.818, p = 0.001, d = 0.853$). Taken together, the vCDA,

404 a neural marker indexing maintenance of information in visual WM (Luck and Vogel, 2013)
405 was present for both stimulus types.

406



407

408 **Figure 3** *Visual encoding of images*: Results of visual potentials locked to the memory array.

409 (A) Contralateral minus ipsilateral visual-evoked potentials pooled over lateral occipital and

410 posterior parietal electrodes (midway between POz and PO3, PO7 and P3; POz and PO4, PO8

411 and P4; visual ROI in figure 1A) for each memory load and stimulus type. Analysis of

412 variance yielded a significant difference between memory loads 1 and 2 in both stimuli types.

413 Large grey squares indicate time windows for statistical analyses; vCDA: visual contralateral

414 delay activity. (B) Topography of the vCDA after onset of the memory array in load 2,

415 showing an occipital-parietal peak in the time window 300-800ms. Topographical maps show

416 contralateral minus ipsilateral amplitude differences projected on the right hemisphere. (C)

417 Differential activity between contralateral minus ipsilateral activity in load 2 minus load 1 for

418 both stimuli conditions. Error bars represent within subject SEMs; n=20. Notwithstanding

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

424

425 *3.3. Motor encoding of images: Motor cortical potentials from visual-motor trials (locked to* 426 *motor response)*

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

437 MCPs in form of sharp preceding motor activity were clearly visible over
438 frontocentral and frontal regions in both stimuli conditions. We computed mean amplitudes
439 after deduction of visual activity elicited in visual-only trials to the visual-motor trials in the
440 time window from -500 to -50ms (0ms: participants' motor response). MCPs elicited over
441 contralateral and ipsilateral to the cued hemifield were analysed for both memory loads and
442 stimulus conditions across frontocentral (C1 and FC1/midway between C1 and FC2,
443 FC3/FC4, FC5/FC6) and frontal ROIs (F1/F2, F5/F6, and AF3/AF4 of the 10/20 system)
444 (Kranczioch et al., 2009; Smith and Staines, 2012; Smulders and Miller, 2012). Specifically,
445 repeated measures ANOVA with hemisphere (contralateral, ipsilateral), memory load (1,2),

446 stimulus type (hand, shapes), ROIs (frontocentral, frontal), and electrode (3 electrodes)
447 yielded main effects of ROI ($F_{(1,19)} = 32.251, p < 0.001, \eta_p^2 = 0.629$) and electrode ($F_{(2,38)} =$
448 $10.149, p = 0.002, \eta_p^2 = 0.348$), significant double interactions between stimulus type and
449 hemisphere ($F_{(1,19)} = 4.931, p = 0.039, \eta_p^2 = 0.206$), hemisphere and electrode ($F_{(2,38)} = 4.979,$
450 $p = 0.012, \eta_p^2 = 0.207$), load and ROI ($F_{(1,19)} = 8.906, p = 0.008, \eta_p^2 = 0.319$), and significant
451 triple interactions between load, hemisphere, and ROI ($F_{(1,19)} = 6.769, p = 0.018, \eta_p^2 = 0.262$)
452 and stimulus type, hemisphere, and electrode ($F_{(2,38)} = 4.630, p = 0.027, \eta_p^2 = 0.195$).
453 Crucially, we also found a significant interaction between all factors ($F_{(2,38)} = 5.995, p =$
454 $0.005, \eta_p^2 = 0.239$). We followed up this latter interaction separately for each hemisphere. In
455 the ipsilateral hemisphere we found main effects of ROI ($F_{(1,19)} = 28.962, p < 0.001, \eta_p^2 =$
456 0.603) and electrode ($F_{(2,38)} = 9.122, p = 0.003, \eta_p^2 = 0.324$). The factor stimulus approached
457 significance ($F_{(1,19)} = 3.362, p = 0.082, \eta_p^2 = 0.150$). No other significant effects and
458 interactions were found (all $ps > 0.05$). In the contralateral hemisphere, we found main effects
459 of ROI ($F_{(1,19)} = 34.451, p < 0.001, \eta_p^2 = 0.644$) and electrode ($F_{(2,38)} = 11.392, p < 0.001, \eta_p^2 =$
460 0.374). Interestingly, the results showed a marginal interaction between stimulus type and
461 ROI ($F_{(1,19)} = 4.209, p = 0.054, \eta_p^2 = 0.181$), which reached significance in interaction with
462 load: stimulus type x ROI x load ($F_{(1,19)} = 6.046, p = 0.024, \eta_p^2 = 0.241$).

463 Given this interaction over the contralateral hemisphere between stimuli types, ROI
464 and load, we proceed to examine the modulation of memory load by ROI for each stimulus
465 condition. For shape stimuli, no main effect of load ($F_{(1,19)} = 0.093, p = 0.763, \eta_p^2 = 0.004$) or
466 interaction between load and ROI ($F_{(1,19)} = 0.162, p = 0.692, \eta_p^2 = 0.008$) were found. The
467 results only showed a main effect of ROI ($F_{(1,19)} = 58.942, p < 0.001, \eta_p^2 = 0.756$), indicating
468 a significant difference between the frontocentral and more frontal ROI regardless of memory
469 load ($t_{(1,19)} = 7.678, p < 0.001, d = 1.716$). Contrary, maintaining hand images in WM elicited
470 mean amplitudes that were distinctively modulated across ROIs ($F_{(1,19)} = 13.573, p < 0.002,$
471 $\eta_p^2 = 0.416$) depending on the number of hand images (i.e. hands) to be remembered ($F_{(1,19)} =$
472 $20.811, p < 0.001, \eta_p^2 = 0.522$). Follow up of analyses separated by ROIs showed a significant

473 difference of mean amplitudes in the frontal ROI when holding one hand vs. two hands ($t_{(1,19)}$
474 = 3.260, $p = 0.004$, $d = 0.743$; in contrast, frontocentral ROI ($t_{(1,19)} = -.676$, $p = 0.507$, $d = -$
475 0.151) (Figure 4A).

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

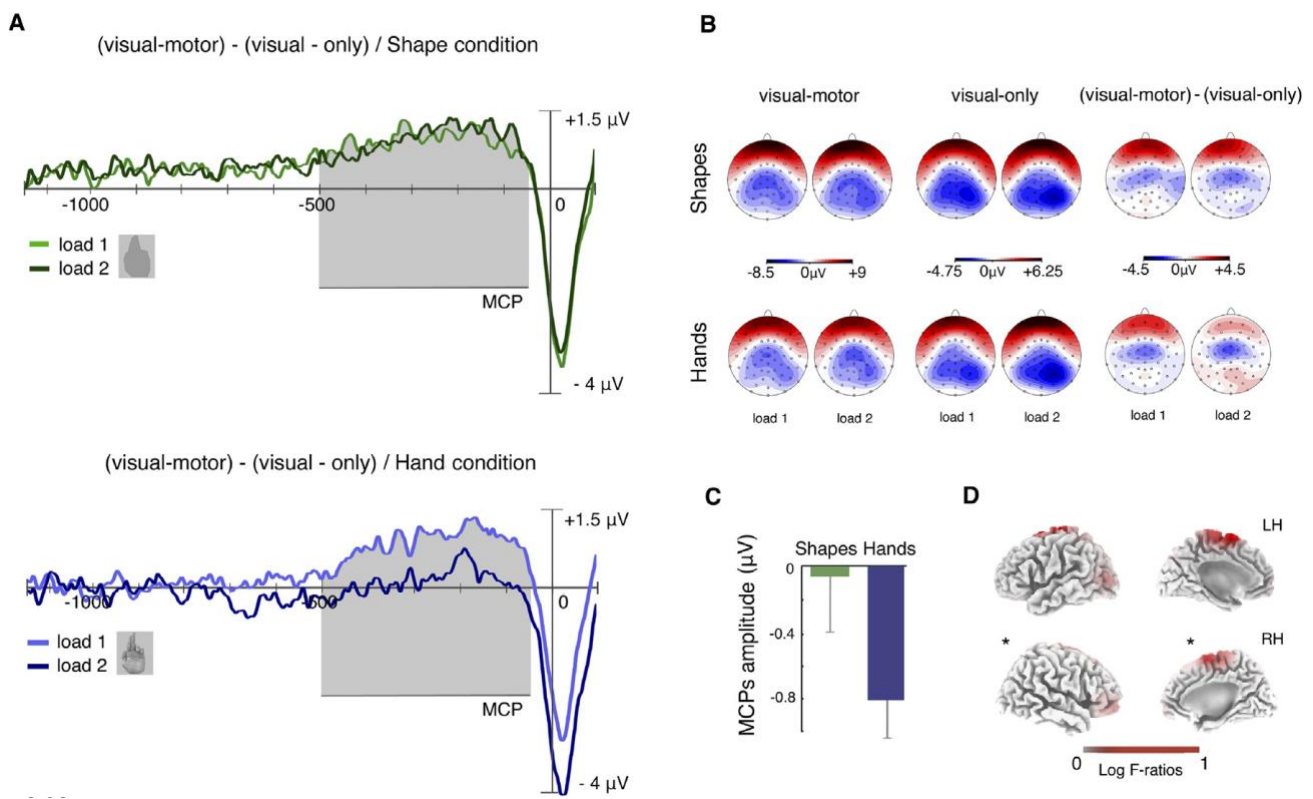
484 Taken together, MCPs modulated by memory load were found in the hand stimulus
485 condition whereas no modulation by load was found in the shape stimulus condition.
486 Importantly, mean amplitudes over frontal electrode sites of the hemisphere contralateral to
487 the hand stimuli to-be-remembered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

492 3.4. Electrophysiological source localization

493 Based on the scalp-recorded electric potential distribution, the Standardised Low-
494 Resolution Brain Electromagnetic Tomography (sLORETA) (Pascual-Marqui, 2002) was
495 used to estimate cortical source estimation. It was performed on the MCPs (response-locked
496 potentials, -500 to -50ms) after subtraction of visual-evoked potentials from visual-only trials,
497 as well as after obtaining the differential brain activity between stimuli types once subtracted
498 memory loads (i.e., load 2 minus load 1 for each stimulus type). This identified a set of
499 candidate regions where maximum differential activity was due to load differences between

500 stimuli conditions including classic motor cortical regions, in precentral and superior frontal
 501 gyrus (Brodmann areas 6/4), and postcentral gyrus over parietal lobe (BA 3). These comprise
 502 premotor cortex, SMA, primary motor cortex, and primary somatosensory cortex over caudal
 503 postcentral regions (Figure 4D).

504



506 **Figure 4** *Motor encoding of images*: Results of finger response-locked motor-cortical
 507 potentials (MCPs). (A) Contralateral waveforms pooled over frontal electrodes (F1/F2, F5/F6,
 508 and AF3/AF4; frontal ROI in figure 1A) for each memory load and stimulus conditions after
 509 subtracting activity from the visual-only trials to the visual-motor trials. Motor preceding
 510 activity can be observed nearly half second before the actual motor response (0ms). A
 511 significant difference of mean amplitudes modulated by memory load was only found in the
 512 hand stimulus condition. No differences were found in the shape stimulus condition. (B)
 513 Whole topographical maps in all conditions, including task, memory load, stimulus
 514 conditions, and the subtraction of visual only trials' activity to visual-motor trials' activity (-
 515 500 to -50ms). (C) Differential activity between load 2 and load 1 for both stimuli conditions.

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

520

521 3.5. Signal-to-noise ratio.

522 Given the subtractive nature of our methodology, it is possible that variance in the
523 signal-to-noise ratio in the subsequent conditions could bias our analyses and results between
524 stimuli types. To rule out this possibility, we also examined the number of accepted trials
525 separately for trials cued to left and right hemifield, for each memory load and type of
526 stimulus in the *visual-motor* and *visual-only* conditions. The only significant results were
527 found as main effects of task (visual-only, visual-motor) ($F_{(1,19)} = 5.695, p = 0.028, \eta_p^2 =$
528 0.230) and load (1,2) ($F_{(1,19)} = 123.394, p < 0.001, \eta_p^2 = 0.866$). No main effects of cue ($F_{(1,19)}$
529 $= 0.780, P = 0.388, \eta_p^2 = 0.019$), stimulus conditions ($F_{(1,19)} = 0.633, p = 0.436, \eta_p^2 = 0.032$),
530 nor significant interaction between all factors was found (all $p_s > 0.067$). These results denote
531 that signal-to-noise ratio did not bias the results on later subtractions across stimuli
532 conditions. The dissimilarities of mean amplitudes over sensorimotor regions sites would be
533 likely due to effects of memory load when processing visual information conveying
534 distinctive properties (body and non-body-related).

535

536 4. Discussion

537 In the current study we examined the neural recruitment of visual and sensorimotor
538 brain areas in a WM task where the stimuli to-be-remembered were body and non-body-
539 related stimuli. We developed a novel paradigm combining findings in WM, action
540 perception, and embodiment. Namely, sensory recruitment models of WM, which postulate
541 that brain areas with a role in the perception of the stimuli are also involved during the

542 consolidation of these in WM (D'Esposito and Postle, 2015; Postle, 2006; Serences et al.,
543 2009), as well as embodiment and internal motor simulation approaches suggesting that
544 visually perceiving bodily information engages one's body representation in sensorimotor
545 cortex (Calvo-Merino et al., 2006; Urgesi et al., 2007). From these two approaches surges our
546 hypothesis regarding the potential involvement of motor cortices during consolidation of
547 body-related stimuli in visual WM. To test this, we integrated for the first time a classical
548 index of motor activation (namely motor-cortical potentials, MCP), in a visual working
549 memory task of body images. Specifically, we evoked visual and motor-cortical potentials in
550 a delayed-match-to-sample paradigm where stimuli to-be-remembered were images
551 conveying different degrees of sensorimotor information (body and non-body-related images;
552 hand vs. shape).

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

560 Importantly, motor activity was examined via MCPs that were elicited through a self-
561 initiated bimanual key pressing task that was irrelevant for the mnemonic task and executed
562 during the active maintenance of the visual images in WM. This manipulation elicited a
563 motor neural signature (namely MCPs) over frontal electrode sites in both hemispheres for
564 both stimulus conditions. Subsequent analyses revealed that only the hemisphere contralateral
565 to the encoded hemispace exhibited a modulation of mean amplitude by memory load and
566 stimulus type. Remarkably, only in the hand stimulus condition the modulation of MCPs by
567 memory load was present; this involves the interaction of a neural signature source localised
568 in motor brain areas (Ikeda et al., 1992; Lu et al., 2012; Shibasaki and Hallett, 2006; Yazawa

569 et al., 2000) with memory load conveyed in the visual stimuli. This latter finding goes beyond
570 classical accounts of embodiment that stress the importance of our own body and motor
571 representations in the perception of body-related information (Calvo-Merino et al., 2006; De
572 Vignemont, 2011), and provides evidence of the engagement of motor cortices during the
573 encoding and maintenance of body-related information in a visual WM task.

574 *4.1. Recruitment of motor cortex in a visual working memory task of body-related information*

575 Premotor cortex, SMA, and the primary motor cortex have been linked to the
576 perception of body-related information (e.g., kinematics, biological motion, body images), as
577 well as sensory guidance of movement and control of the body, sequencing, planning,
578 initiating, learning, and imagining movements. Evidence for this comes from
579 electrophysiological studies reporting modulation of MCPs over sensorimotor brain regions
580 when observing other's actions (Holländer et al., 2011; Kilner et al., 2004; van Schie et al.,
581 2004) and when preparing or imagining hand actions with different level of motor complexity
582 (Kranczioch et al., 2010, 2009). Likewise, neuroimaging studies have shown long lasting
583 effects of body experience (i.e., a form of motor long-term memory) in sensorimotor cortex
584 during action observation (Calvo-Merino et al., 2006, 2005; Orgs et al., 2008), as well as
585 modulation of activity in motor cortex related to the affordability of the objects to be
586 maintained in WM (Mecklinger et al., 2004, 2002). Here, we provide new evidence
587 supporting the involvement of motor cortex in visual high-order cognitive processes beyond
588 perception. Importantly, the combination of visual and motor evoked responses within the
589 same trial and the isolation of superimposed neural components (Galvez-Pol et al., 2018; Sel
590 et al., 2014; Talsma and Woldorff, 2005) provides this motor response a significant role in
591 visual working memory over and above potential carry over effects from visual processing.

592 Our results are consistent with earlier work in visual WM suggesting how neural
593 recruitment across cortical regions depends on the stimuli's features to-be-remembered
594 (Gazzaley et al., 2004; Lee et al., 2013; Serences et al., 2009). Here we compared body-
595 related visual information with analogous non-body-related information (hand vs. shape

596 conditions). While both stimulus conditions show similar behavioural performance and
597 engagement in visual sensory cortices, we find differences between the hand and shape
598 conditions in the modulation of the motor cortical responses. We attribute this MCP
599 differences to recruitment of sensory associations related to the memoranda rather than to a
600 mere effect of complexity during early visual processing (Brady et al., 2016; Galvez-Pol et
601 al., 2018; Konkle and Brady, 2010; McWeeny et al., 1987).

602 *4.2. Present challenges and forthcoming questions*

603 Our results show modulation of visual-evoked potentials for the two stimulus
604 conditions, but only WM maintenance of body-related images modulates MCPs. One
605 interesting question arises from the relationship between this specific modulation and its
606 relationship with the mnemonic content of the perceived stimuli. Previous behavioural
607 studies reported that WM maintenance of visually perceived actions is impaired when a
608 concurrent body-related task is performed. Interestingly, this effect has been observed
609 whether the actions need to be reproduced (Smyth et al., 1988; Smyth and Pendleton, 1989)
610 or visually recognized in a delayed-match paradigm (Moreau, 2013; Wood, 2007). Moreover,
611 WM for body-related information is also impaired by secondary task that involve active
612 maintenance, as well as mere perception of additional body stimuli (Smyth and Pendleton,
613 1990). More recent studies highlight content-specific processing across both visual and motor
614 cortices. Two cortical pathways have been identified in the processing of identity and motion
615 information in occipitotemporal regions (extrastriate body area, EBA) and premotor cortices
616 (Urgesi et al., 2007). On a similar note, Wurm and Lingnau (2015) showed that during action
617 observation brain activity in inferior parietal and occipitotemporal cortex can be decoded for
618 the abstract levels of the observed actions whereas activity in the premotor cortex can be
619 decoded for their concrete levels (i.e., specific kinematics). Our results provide a stepping-
620 stone to studies investigating the specific features of the body stimuli that motor cortices
621 encode and maintain in visual working memory.

622

623 4.3. Conclusion

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

640 **Author contributions**

641 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
642 B.F. analysed and interpreted the data; A.G-P and B.C.-M wrote drafts of the manuscript, and
643 B.F provided critical comments on the paper.

644 **Ethics**

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

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652

653 **The authors declare no conflict of interest.**

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