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

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Abstract

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

Highlights

- Dissociation of somatosensory-evoked potentials (SEPs) from visual processing of body-related images in WM

- Distinctive modulation of SEPs by memory load only during maintenance of body-related stimuli

- Type of information embedded in the visual stimuli summons specific processing resources (embodiment mechanisms acting upon WM processes).

1. Introduction

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

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

examined WM mechanism for body-related images had already suggested that internal bodily/sensorimotor representations contribute to perceive and maintain in memory visually perceived body-related information (Shen et al., 2014; Smyth et al., 1988; Smyth and Pendleton, 1990, 1989; Wood, 2007).

Based on the aforementioned models proposing similar neural mechanisms for perception and memory and the studies showing recruitment of body-related cortices during perception of bodies, we investigated whether the active maintenance of body-related images in WM elicits neural recruitment of visual regions (as previously described for simple images of shapes) and other sensory regions that participate in the representation of body-related information in the brain (i.e., somatosensory cortex, SCx). To this aim, we examined persistent activity (a neural marker of attention based rehearsal) during a WM task for body and non-body-related images. Persistent activity, also known as sustained or delay activity, is usually observed between the memory and test phases (i.e., during the retention interval) in sensory areas relevant for the task. A key feature of this activity is that it persists in the absence of continued sensory input. Moreover, its amplitude is modulated by the number of stimuli to-be-remembered (memory load) (Luria et al., 2016; Todd and Marois, 2004; Vogel and Machizawa, 2004). In the current study, we recorded persistent activity within visual and somatosensory-evoked potentials (VEPs, SEPs) in a visual WM task where participants were instructed to memorise images of hands and matching polygonal shapes (Figure 1a and 1c). Similar to previous studies of WM for visually perceived stimuli (McCollough et al., 2007; Tsubomi et al., 2013; Vogel and Machizawa, 2004), we recorded trials containing VEPs elicited by the visual onset of the images to-be-remembered (visual-only trials). Importantly, we also probed the state of SCx by using task-irrelevant tactile taps that were delivered to the participants' fingers in synchrony with the onset of the images to-be-remembered. The resulting activity contained brain activity due to visual and somatosensory-evoked potentials (visual-tactile trials). While the analyses of VEPs from visual-only trials allowed us to examine persistent activity arising from occipito-parietal visual regions, it also enabled us to

examine SCx processing by subtracting brain activity of the visual-only trials to the compound activity of the visual-tactile trials (see Sel et al., 2014). This subtraction (Figure 1b) allowed us to reveal an ERP component that has not been described yet in the WM or action observation literature, a visually driven component in the form of persistent activity reflecting encoding and maintenance of visual information of body images beyond visual areas in SCx.

2. Materials and Methods

2.1. Participants

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

2.2. Stimuli

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

2.3. Experimental design and procedure

Participants performed a visual memory task similar to that of Vogel and Machizawa (2004). Items to-be-remembered were hand images (depicting different finger/hand positions) and analogous geometrical shapes (Fig. 1B). Participants were cued on each trial by a central arrow to attend to items displayed in their left or right hemifield. This was followed by a bilateral memory array depicting 1 or 2 items (low and high memory load conditions) in each hemifield and a blank retention interval lasting 900ms. A final test array that differed in 50% of the cases from the memory array by one item was displayed until participants verbally

responded whether or not the memory and test arrays were identical (Fig. 1A). The participants' verbal responses were reported through a microphone to the experimenter, who entered the responses manually from outside of the electromagnetically shielded room. Participants' forearms rested on the top of a table with their hands separated in palm up position while covered by a black surface. Visual stimuli were displayed using E-Prime2 Software (Psychology Software Tools, Pittsburgh, PA).

All stimulus arrays were presented within two 5° x 8.5°rectangular regions that were centred 5.3° to the left and right of a central fixation cross on a grey background. The positions of all stimuli were randomized on each trial with the constraint that the distance between stimuli within a hemifield was at least 2.4° (centre to centre). Each memory array consisted of 1 or 2 hands (1.3° x 0.8°) in each hemifield. These were randomly selected from a set of twelve hands. Right hand images were shown on the right hemifield while left hand images were displayed on the left. The rationale behind this latter choice is based on the clear contralateral brain representation of the hands in the somatosensory cortex. This allows the possibility of measuring persistent contralateral activity over SCx, which can be isolated from concomitant visually evoked activity when seeing and remembering the stimuli. In the control condition, 1 or 2 polygonal shapes (1.3° x 0.8°) were selected and shown in a similar fashion. Since prior studies have shown that remembering two items may well lead to limits in WM capacity (Alvarez and Cavanagh, 2004; Luria et al., 2010; Olsson and Poom, 2005); memory load 1 and 2 (low/high) would allow observing increasing activity related to memory encoding and maintenance.

Visual-only trials. In 50% of the trials, only VEPs were elicited. These were recorded from the onset of the visual memory array and while participants maintained in working memory the stimuli until the test array appeared.

Visual-tactile trials. In the other 50% of the trials, we elicited simultaneously VEPs and SEPs by applying task-irrelevant single tactile taps simultaneously delivered to both hands on the tip of the participants' index fingers at the onset of the visual memory array. Tactile

stimulation was applied using two 12 V solenoids driving a metal rod with a blunt conical tip that contacted with participants' skin when a current passed through the solenoids. Both solenoids were placed on the tip of the index fingers, one for each hand. To mask sounds made by the tactile stimulators, white noise (65 dB, measured from participants' head) was presented through a loudspeaker centrally positioned 90cm in front of the participants. Participants were instructed to ignore these tactile stimulations.

2.4. ERP Subtraction

When persistent activity is recorded through extracellular field recordings via event-related-potentials and electroencephalography (ERP-EEG), it is computed by time locking the stimuli to-be-remembered to a single evoked sensory modality. For instance, in a WM task for stimuli such as coloured squares, persistent activity is obtained over posterior visual electrodes by time locking the consolidation interval of the stimuli in WM to those visual-evoked potentials (VEPs) elicited at the onset of the stimuli to-be-remembered (see for instance, McCollough et al., 2007; Luria et al., 2016). However, in a WM task for body-related images, the VEPs that are also elicited at the sight of these stimuli spread from posterior to more anterior cortices, superimposing brain activity from different neural generators (Ahlfors et al., 2010; Irimia et al., 2012; Luck, 2014), and likely masking persistent activity over body-related cortices (i.e., SCx) that may be responsible for processing body-related information. To overcome this issue, we applied mechanical stimulation in the form of tactile taps in the visual-tactile condition. This allowed us to examine the state of the SCx, exposing its underlying processing during memory encoding and maintenance of the visual stimuli by measuring the electroencephalographic activity of SEPs elicited by task-irrelevant tactile stimulation. These tactile taps probe the responses of the SCx during encoding and maintenance of the visual stimuli. Moreover, to be able to isolate somatosensory processing over corresponding parietal electrode sites from superimposing visual activity elicited by the visual onset of the stimuli, we subtracted brain activity from those trials containing activity only due to VEPs (visual-only trials) to those

trials containing a combination of visual and somatosensory activity due to the combined VEPs-SEPs (visual-tactile trials). This allows isolating and observing somatosensory processing free of visually evoked activity, that is, visually driven activity in the form of SEPs VEPs-free (Sel et al., 2014).

Overall, participants performed a total of 1344 trials, 672 for each stimulus condition (hands and geometrical shapes). This is equal to 336 trials for each load condition (low and high): half of the trials entailed the presentation of task-irrelevant tactile taps (visual-tactile trials) while the other half involved visual only trials (visual-only trials). The following experimental manipulations were randomly presented to the participants on trial by trial basis: memory load, type of stimulation, side of the cue, and location of the stimuli on the screen. The order of the stimulus conditions was counterbalanced across participants.

2.5. ERP recording and data analysis

The study was performed in an electromagnetically shielded room using a 75Hz LCD monitor. 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 earlobe and re-referenced off-line to the average of all electrodes. Vertical and bipolar horizontal electro-oculogram were recorded for eye movements tracking and artifact correction purposes. For this, electrodes were placed ~1cm to the outer canthi of each eye (horizontal electro-oculogram) and below and above the right eye (vertical electro-oculogram). Continuous EEG was recorded at 500 Hz using a BrainAmp amplifier (Brain Products GmbH, Gilching, Germany; amplifier bandpass 0.06-100 Hz). Off-line EEG analysis was performed using Vision Analyzer software (Brain Products GmbH, Gilching, Germany). The data were digitally low-pass-filtered at 30 Hz (Butterworth zero phase filters) and ocular correction was performed by subtracting the voltages of the ocular channels, multiplied by a channel-dependent correction factor from the EEG channels, calculated by linear regression (Gratton et al., 1983; Miller et al., 1988). Segments were then baseline corrected to 200ms before the

onset of the memory array and the segments including other artifacts (a voltage exceeding ± 85 µV at any of the electrode relative to baseline) were excluded. The EEG signal was epoched into 1300ms segments, starting 200ms before the sample arrays of each trial. Grand averages were computed independently for the hand and shape stimulus conditions on correct response trials, separately for the two memory loads and for visual and visual-tactile trials by averaging brain waveforms elicited at electrodes over the hemisphere contralateral and ipsilateral to the items to-be-memorized as indicated by the central cue. The average number of correct response trials that entered the analyses after pre-processing of the data was 66% in both stimulus conditions, this is equal to an average of 109 epochs by condition ($SD = ±17$) in the shape stimulus condition and likewise 109 epochs ($SD = ±18$) in the hand stimulus condition (see Supplementary Table 1 for the total number of accepted trials included in the analyses).

We took advantage of the contralateral disposition of the visual system by comparing persistent activity in the contralateral and ipsilateral hemispheres to the hemifield containing the stimuli to-be-remembered (as indicated by the arrow). We examined this activity (i.e., visual contralateral delay activity, CDA) over occipito-parietal electrodes during the consolidation interval of the stimuli in visual-only trials. The CDA was computed by comparing the mean amplitude of contralateral and ipsilateral activity in the time window 300-900ms after stimulus onset for each memory load (Vogel and Machizawa, 2004). More specifically, when participants were cued to the left side of the memory array we averaged mean amplitudes recorded at electrodes of the right hemisphere and left hemisphere as contralateral and ipsilateral, respectively. The reversed disposition was applied when participants were cued to the right side (i.e., left and right hemispheres as contralateral and ipsilateral, respectively). The comparison of contralateral and ipsilateral activity allowed lessening contributions of nonspecific bilateral neuronal activity. We calculated mean amplitudes separately for the low and high loads in the shape and hand stimulus conditions (see supplementary information – methods). Statistical analysis was performed for mean

amplitudes at occipital and posterior parietal electrode sites (O1, O2, midway between PO7/P7, and midway PO8/P8 of the 10-20 system) (McCollough et al., 2007; Vogel et al., 2005; Vogel and Machizawa, 2004). Mean amplitudes were compared across conditions by analysis of variance (ANOVA).

We also computed contralateral waveforms of somatosensory processing from trials in the visual-tactile condition. The visually driven contralateral delay activity (vdCDA) was computed by comparing the mean amplitudes of contralateral (e.g., activity in right hemisphere electrode sites when cued to the left side and vice versa) and ipsilateral activity in the time window 300-900ms after stimulus onset for each memory load. The underlying activity of somatosensory cortices when maintaining in memory visually acquired stimuli were analysed over parietal electrode sites at CP3/CP4 and CP5/CP6 of the 10-20 system. Then, to isolate somatosensory processing from the visual activity elicited by the onset of the stimuli on the screen, we removed VEPs by subtracting mean voltage amplitude of averaged VEPs on visual-only trials to the mean amplitudes of averaged event-related potentials on visual-tactile trials (containing both somatosensory and visual-evoked potentials; SEPs and VEPs). This subtractive methodology based on evoked activity from different neural sources has been commonly used to study multiple sensory modalities (Senkowski et al., 2007; Talsma et al., 2010; Talsma and Woldorff, 2005). In our specific case, to test SCx encoding of hands driven by the onset of the visual array, synchronously to VEPs, SEPs elicited by task-irrelevant tactile stimulation were employed (Sel et al., 2014). Under such conditions, evoked activity would contain a contribution from both sensory cortices elicited by VEPs and SEPs. This leads to the use of an only VEPs condition, which allows i) the examination of brain activity of visual cortices, ii) the subtraction of visual carry over effects over somatosensory cortices, and the consequent analysis on iii) effects of memory load over both cortices. We first analysed the vdCDA in the time window of the retention interval (300-900ms after stimulus onset). Moreover, we also tested the steadiness of this extensive persistent activity by examining the time course along its whole length in six consecutive bins

of 100ms. Lastly, we inspected the preceding activity in the time window of 200-300ms. We examined this period because its activity has been previously associated to the allocation of attentional resources for the selection of task-relevant stimuli in attentional and WM paradigms (Eimer, 1996). When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were applied. To correct for multiple comparisons in the analyses of the vdCDA and the mean amplitudes included in the 200-300ms time window, the significance level was Bonferroni-corrected (corrected P values: 0.05/2).
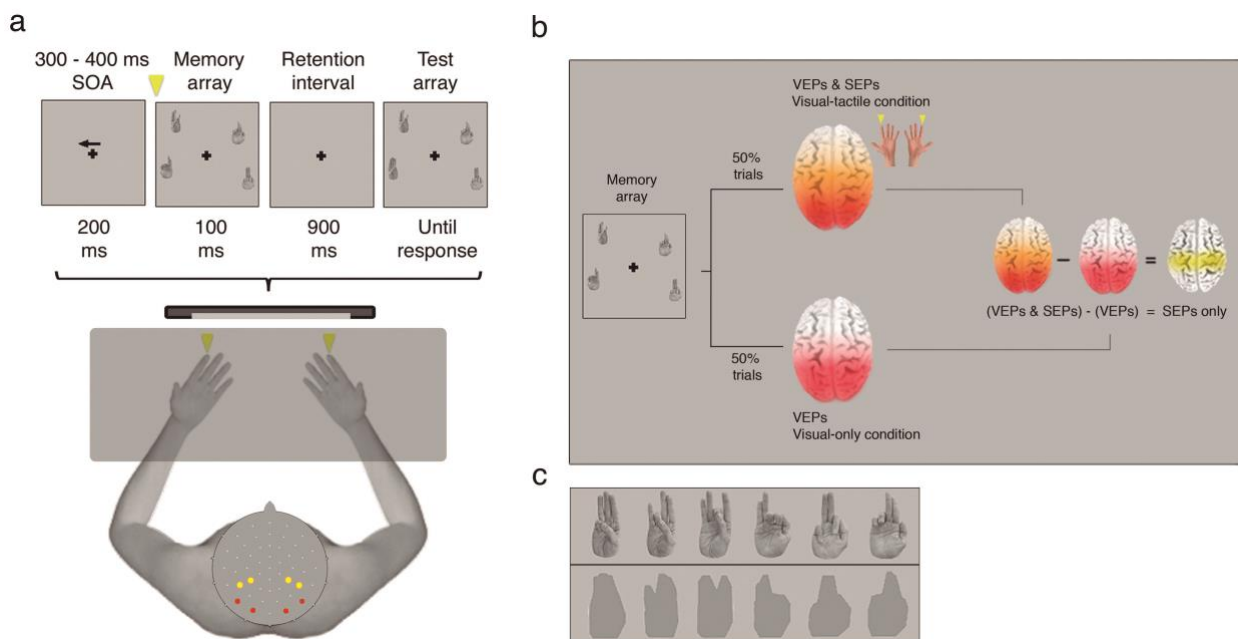

Figure 1. Task design, schematic illustration of subtractive methodology using SEPs and VEPs, and example of stimuli. (a) All participants performed a WM task for body-related images (hands) and control, non-body-related images (shapes). Participants verbally responded whether or not the stimuli in the left or right hemifield (as indicated by the arrow) were the same in the memory and test arrays. Half of the trials included task-irrelevant tactile stimulation delivered to both index fingertips at the onset of the memory array (yellow triangles). The yellow dots in the mannequin's head indicate the electrode sites included in the analyses of SEPs whereas the red dots indicate the sites analysed for VEPs. (b) Schema of the subtraction methodology employed to isolate SCx processing from visual carry over effects elicited after the perception of the memory array. The visual-tactile condition (50% of trials) included VEPs elicited at the onset of the visual array and somatosensory evoked potentials (SEPs)

elicited by task-irrelevant tactile stimulation applied simultaneously at the onset of the visual memory array (central-upper section). The visual-only condition (50% of trials) consisted of only VEPs (central-bottom section) elicited at the onset of the visual array. The subtraction illustrated on the right [visual-tactile condition]-[visual-only condition] allows dissociating SCx from the concurrent visual activity. (c) Example of 6 grey scaled right hands depicting different hand/finger positions and homologous shapes stimuli.

2.6. ERP signal-to-noise ratio

To examine the levels of signal-to-noise ratio across our different experimental conditions a repeated-measures ANOVA on the number of accepted trials with the factor memory load (low/high), cue (trials cued to the left/right hemifield), stimulation condition (visual-only/visual-tactile trials) and stimulus condition (hand images/shapes) was conducted. The results showed no main effects of cue ($F_{(1,19)} = 1.017$, $P = 0.326$), stimulation ($F_{(1,19)} = 0.727$, $P = 0.404$), stimulus ($F_{(1,19)} = 0.000$, $P = 0.997$), nor interaction of these factors ($F_{(1,19)} = 0.122$, $P = 0.731$). These analyses confirm that the signal-to-noise ratio was not different in our two main stimulation conditions and this could not bias the results in later subtractions. Specifically, subtraction of VEPs elicited on the visual-only trials from the conjunction of VEPs and SEPs elicited on visual-tactile trials would therefore subtract out brain activity equally present in both conditions while exposing concealed effects of visually driven processing in somatosensory areas.

2.7. Current source density analysis (CSD).

We estimated the neuronal generator patterns contributing to our results by transforming the scalp-recorded EEG to surface Laplacians. Such transformation leads to a conservative estimate of the neuronal generator patterns underlying the EEG in which regardless of the orientation, location, number, or extent of active neural tissue, the effects of volume conduction from distant sources are reduced and a reference-independent representation of EEG/ERP data is obtained (Perrin et al. 1989; Nunez and Westdorp 1994; Tenke and Kayser

2012). CSD was obtained by transforming scalp potentials from voltage distribution on the surface of the head to surface Laplacians, here the voltage levels in µV were transformed to µV/m2; lambda 10-5, order of splines m: 4, legendre polynomial: 10 (Nunez and Westdorp 1994; Katus, Grubert, and Eimer 2015). As voltage distribution is known at the electrodes, the procedure of spherical spline interpolation was used to compute the total voltage distribution.

The CSD topographical maps of the visually driven CDA (vdCDA, VEP-free) were calculated as the earlier scalp-recorded EEG data by computing contralateral and ipsilateral mean amplitudes for the low and high memory load in the hand stimulus condition in the 200-300 and 300-900ms time windows after onset of the sample array. Statistical analysis was performed by analysis of variance and included mean averages of electrode sites along the different ROIs in the scalp from anterior to posterior regions, respectively of the 10-20 system: midway between F7/AF7 - F8/AF8, and AF3/AF4; F5/F6 and F1/F2; FC5/FC6 and FC3/FC4; C5/C5 and C3/C4; CP3/CP4 and CP5/CP6; midway between PO3/P5 - PO4/P6, and P1/P2; midway between PO7/P7 - PO8/P8, and O1/O2. When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were applied. To account for multiple comparisons in the analyses of the mean CSD amplitudes in the vdCDA and the 200-300ms time windows, the significance level was Bonferroni-corrected (corrected *P* values: 0.05/2).

3. Results

3.1. Behavioural performance

Participants correctly reported similarities or differences between the memory and test arrays in the cued hemifield in 77.5% of all trials of the hand stimulus condition and in 76.8% of all trials of the shape stimulus condition. Moreover, they correctly reported similarities or differences between the memory and test arrays in 77.3% of all trials in the visual-only condition and in 77.4% of all trials in the visual-tactile condition. Analysis of sensitivity index *d'* (Stanislaw and Todorov, 1999) was computed in a three way repeated-measures ANOVA with the factors stimulus (shapes/hands), stimulation condition (visual-only/visual-

tactile), and memory load (low/high). The results showed a significant main effect of memory load ($F_{(1,19)}$ = 251.276, p < 0.001), no main effects of stimulus condition ($F_{(1,19)}$ = .022, P = 0.883) nor stimulation condition (visual-only/visual-tactile) ($F_{(1,19)}$ = .078, P = 0.782). A significant interaction between stimulus type and memory load reached significance ($F_{(1,19)}$ = 11.108, p = 0.003). We followed up this interaction by separately comparing each type of stimulus for low and high memory load. Significant differences were not found for either memory load ($t_{(1,19)}$ = 1.811, p = 0.086 and $t_{(1,19)}$ = -2.087, p = 0.051, respectively). Lastly, the interaction between all factors (i.e., stimulus X load X stimulation) did not reach significance ($F_{(1,19)}$ = 1.076, P = 0.313). Overall, performance was not significantly difference in the hand and shape stimulus conditions (*1.77 d'* in both conditions*; SEM = ±0.09* and *±0.1*, respectively) regardless whether task-irrelevant tactile stimulation was presented or not (Figure 2). Therefore, the analyses confirm the matching of task difficulty for hand images and shapes and no further influence of the presence of task-irrelevant tactile stimuli on task performance.
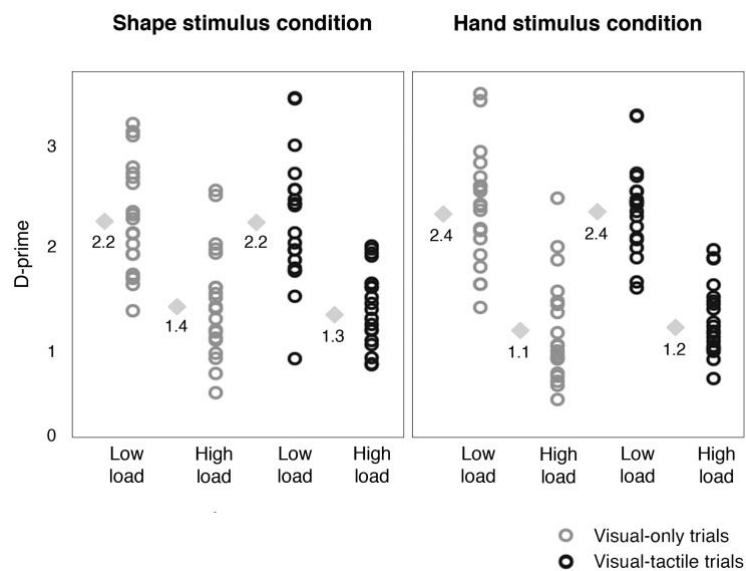

Figure 2. Behavioural results in each condition. Dots represent the means of individual participants, light grey diamonds the group average. Overall performance in hand and shape stimulus conditions were similar and no significant differences were found between performance for low and high memory

loads in the hand and shape conditions regardless the tactile stimulation (all $Ps \geq 0.05$), $n=20$. D-prime: sensitivity index, $d' = Z$ *(hit rate) – Z (false alarm rate)*.

Overall, we aimed to examine distinct recruitment of visual and somatosensory cortex due to the type of information conveyed in the visual stimuli (body *vs.* non body-related) and not because of differences in the discrimination of the stimulus sets nor the effects of task-irrelevant tactile stimulation. To this aim, we ensured the discrimination of the stimulus sets in an earlier pilot experiment and then proceed to analyse behavioural performance across all the conditions in the current study. The analyses confirm the matching of the stimulus sets and no further influence of the stimulation on task performance.

3.2. Visual recruitment during WM: persistent activity from visual-only trials

We examined persistent activity over occipito-parietal electrode sites during the consolidation interval of the stimuli in visual-only trials. We took advantage of the contralateral processing of visual information by comparing brain waveforms in the contralateral and ipsilateral hemispheres to the hemifield containing the array of stimuli to-be-remembered (as indicated by the arrow). Specifically, the data were collapsed across trials where the stimuli in left or right hemifield were task-relevant by averaging together ERPs elicited at electrodes contralateral and ipsilateral to the cued hemifield. We compared increases of persistent contralateral activity during the retention interval (namely, contralateral delay activity; CDA) for low and high memory load in the shape and hand stimulus conditions in the 300-900ms time window after onset of the memory array (Luria et al., 2016; Tsubomi et al., 2013; Vogel et al., 2005; Vogel and Machizawa, 2004). Repeated measures ANOVA on the mean amplitudes was conducted separately for each stimulus condition with the factors hemisphere (contralateral and ipsilateral) and memory load (low and high).

As can be seen in Figure 3, in the shape stimulus condition, persistent activity appeared circa 300ms after the onset of the memory array in occipito-parietal electrode sites

contralateral to the memorized hemifield. This persistent contralateral delay activity (CDA) lasted for the entire consolidation interval and increased with the number of polygonal shapes to be stored in WM. Repeated measures ANOVA showed a significant main effect of load ($F_{(1,19)} = 14.106$, $P = 0.001$), hemisphere ($F_{(1,19)} = 11.679$, $P = 0.003$), as well as a significant interaction between these factors ($F_{(1,19)} = 8.929$, $P = 0.008$). We performed follow-up t-tests comparing brain activity from ipsilateral and contralateral hemispheres in each memory load condition. This showed a significant difference ($t_{(19)} = 4.407$, $P < 0.001$) between mean amplitudes of the ipsilateral and contralateral hemispheres in the high memory load condition (0.2 *vs.* -0.8; *SEM:* ±0.3 and ±0.4). Interestingly, the CDA was also present in the hand stimulus conditions but no interaction between hemisphere and load was found. Repeated measures ANOVA showed significant main effects of load ($F_{(1,19)} = 11.638$, $P = 0.003$) and hemisphere ($F_{(1,19)} = 19.090$, $P < 0.001$), but no significant interaction between these factors ($F_{(1,19)} = 0.184$, $P = 0.673$). These results suggest that the hand stimuli were visually processed in this visual WM task. However, the evoked neural response did not elicit an interhemispheric difference modulated by the load (Figure 3), which is indeed the characterizing feature of persistent CDA as a marker of attention-based rehearsal (Luck and Vogel, 2013).

Footnote 1.

Despite differences in the appearance of the body and non-body-related images, we expect that in this visual WM task, lateralised effects of visual processing should be similar across the stimulus conditions. In the VEPs, we analysed separately the interaction of hemisphere by memory load in each stimulus condition to show how the ipsilateral/contralateral waveforms develop along the time course for each of the conditions. However, the triple interaction between stimulus, hemisphere, and load does not reach significance ($p = .092$).
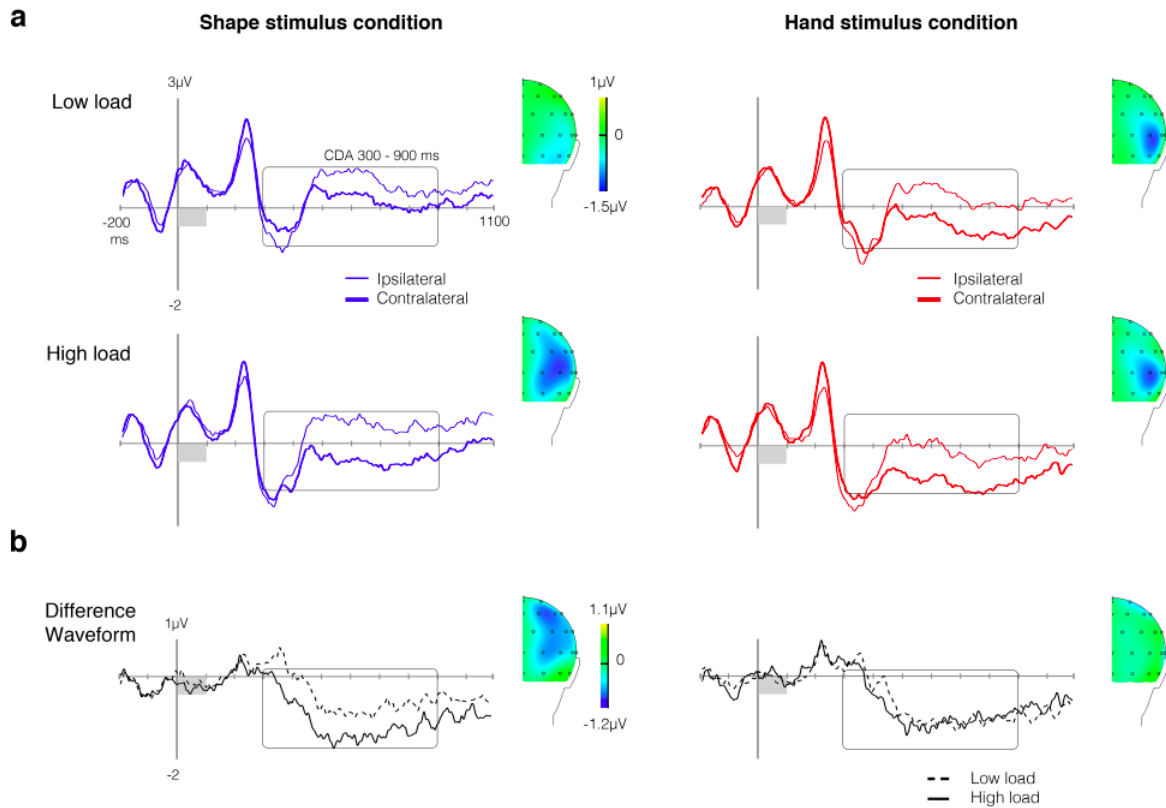
Figure 3. Results of grand averaged VEPs and topographies from visual-only trials separated for the shape and hand stimulus conditions. (a) Contralateral and ipsilateral visual-evoked potentials (VEPs) from posterior electrodes for each memory load and stimulus conditions. Topographies show the amplitude difference between contralateral and ipsilateral recordings in the time window 300-900ms. (b) Difference waveforms show the effect of memory load by subtracting ipsilateral to contralateral waveforms across memory loads (contralateral delay activity –CDA). Increasing persistent activity concomitant to memory load was only found in the shape stimulus condition in the 300-900ms time window ($P = 0.008$). Topographies portray the amplitude difference between high and low load. Grey bars indicate the memory array duration; n=20.

3.3. Somatosensory recruitment during WM: persistent activity from visual-tactile trials minus visual-only trials

We proceed to examine persistent activity over parietal electrode sites during the consolidation interval of the stimuli in the same WM task. In this analysis, we took advantage of the contralateral organisation of SCx and the lateralized processing of visually perceived

18

body-related information in the brain (Buccino et al., 2001; Keysers et al., 2010; Shmuelof and Zohary, 2006) by comparing contralateral and ipsilateral waveforms to the stimuli to-be-remembered. Then, we isolated somatosensory processing from concomitant visual activity by subtracting our stimulation conditions (i.e., visual-tactile minus visual-only trials). This manipulation allows the possibility of examining visually driven processing of information in cortices other than visual, specifically, over SCx (Sel et al. 2014). If consolidation of visually perceived body-related information reflects a truly somatosensory response, then responses of SCx elicited by task-irrelevant tactile taps may be differentially affected by the number of hand images (load) to be held in WM.

After subtraction of visual-evoked potentials, we first inspected the presence of persistent visually driven contralateral delay activation (vdCDA), across ipsilateral and contralateral activity for each stimulus condition, hemisphere (contralateral and ipsilateral), and memory load (low and high). We ruled out an inadequate subtraction of visual activity between our stimulation conditions by inspecting the same occipito-parietal electrode sites that reached significance in the previous analyses of visual-only trials. Here, repeated-measures ANOVA did not reach significance for any of the factors (i.e., hemisphere and memory load across stimulus conditions; all Ps > 0.05) neither did the interaction of these factors in the shape and hand stimulus conditions ($F_{(1,19)} = 1.938$, $P = 0.180$ and $F_{(1,19)} = 0.747$, $P = 0.398$, respectively). These results suggest that visual activity was certainly subtracted from the concurrent stream of visual and somatosensory activity contained in the visual-tactile trials.

Then we proceeded to examine brain activity over more anterior parietal electrode sites. We found a significant interaction between the stimulus condition, hemisphere, and load ($F_{(1,19)} = 10.447$, $P = 0.004$). We followed-up this triple interaction by analysing each stimulus condition separately. In the shape stimulus condition, brain activity over the contralateral and ipsilateral hemispheres to the memorized hemifield did not exhibit any modulation by memory load (Figure 4). Repeated measures ANOVA showed no significant

effects of hemisphere ($F_{(1,19)}$ = 0.053, P = 0.820) or memory load ($F_{(1,19)}$ = 0.001, P = 0.975), nor an interaction between these two factors ($F_{(1,19)}$ = 1.210, P = 0.285). Importantly, in the hand stimulus condition repeated measures ANOVA showed no main effects of hemisphere ($F_{(1,19)}$ = 2.512, P = 0.130) or load ($F_{(1,19)}$ = 0.178, P = 0.678), however, a significant interaction between hemisphere and memory load ($F_{(1,19)}$ = 11.846, P = 0.003) was present reflecting increased persistent activity over the contralateral SCx to the visually cued hemifield as the number of hand images to-be-remembered increased (Figure 4). Follow-up t-tests revealed a significant difference between ipsilateral and contralateral hemispheres' brain activity only in the high memory load condition ($t_{(19)}$ = 2.775, P < 0.012; 0.3 *vs.* -0.3; *SEM:* ±0.16 and ±0.17). This visually driven CDA (vdCDA) revealed in VEP-free SEPs was only present in the hand stimulus condition over parietal electrode sites, whereas no significant modulation by memory load was found when memorizing the non-body-related images of shapes (see Supplementary Table 2 for list of mean amplitudes across conditions). We also investigated the time course of the vdCDA in the hand stimulus condition by analysing six consecutive bins of 100ms time windows from 300 to 900ms after the onset of the stimuli (i.e., analysing the interaction of time window X hemisphere X load). No significant interaction between these factors was found ($F_{(1,19)}$ = .958, P = 0.420), suggesting a steady activity during the retention interval. We also explored the neural response in the 100ms preceding the 300-900ms contralateral persistent activity. Brain activity in the 200-300ms time range has been associated to the allocation of attentional resources during visual search, tracking, and WM tasks (Eimer, 1996). In the 200 to 300ms time window a significant main effect of hemisphere ($F_{(1,19)}$ = 5.607, P = 0.029) and a significant interaction of hemisphere by load ($F_{(1,19)}$ = 16.057, P = 0.001) was present. Follow-up t-tests revealed a significant difference between ipsilateral and contralateral brain activity only in the high memory load condition ($t_{(19)}$ = 3.799, P < 0.001; 1.1 *vs.* 0.5; *SEM:* ±0.2 in both cases). The timing of this lateralized effect resembles that of other well-known ERP negativities (e.g., N2pc and N2cc) that are observed in visual and tactile WM tasks when attending to the contralateral hemispace (Eimer, 1996; Katus et al., 2015). The presence of this lateralized effect, which we

named visually driven N2cc (vdN2cc), suggests that also the topography and neural generators of attentional selection mechanisms present during a WM task depend on the type of information embedded in the visual percept (i.e. somatosensory cortex for the attentional selection of body images).
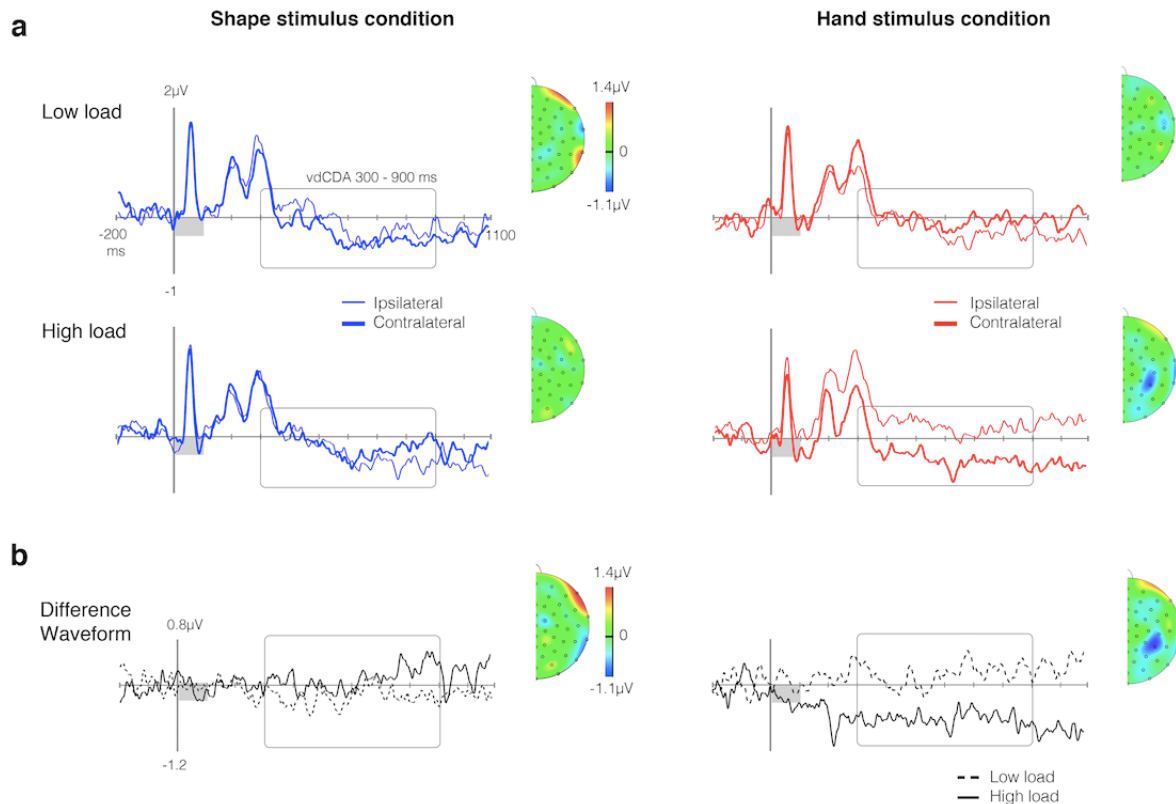

Figure 4. Results of grand averaged evoked-activity after subtraction of visual-only trials from visual-tactile trials (SEPs free of VEPs) and topographies from the top view separated for the shape and hand stimulus conditions. (a) Contralateral and ipsilateral potentials over parietal electrodes for each memory load and stimulus conditions.). Topographies show the amplitude difference between contralateral and ipsilateral recordings in the 300 to 900ms time window. (b) Difference waveforms show the effect of memory load by subtracting ipsilateral from contralateral waveforms for each memory load. Topographies portray the amplitude difference between high and low load. Increasing persistent activity concomitant to memory load was only found in the hand stimulus condition over parietal electrodes in the 300-900ms time window ($P = 0.003$; Visually driven contralateral delay activity –vdCDA). Grey bars indicate the memory array duration; n=20.

3.4. Current source density of somatosensory recruitment in WM

Current source density analysis (CSD) was conducted to examine the underlying sensory specificity of the previous components and to validate the correct selection of lateral-parietal electrode sites. For this purpose, we converted scalp potentials to surface Laplacians. This conversion reduces the effects of volume conduction from distant sources and offers a reference-independent representation of EEG/ERP data. CSD topography offers a conservative estimate of the neuronal generator patterns contributing to scalp-recorded EEG (Nunez and Westdorp, 1994; Perrin et al., 1989; Tenke and Kayser, 2012). We newly isolated the response elicited by the tactile stimulation in VEP-free SEPs (i.e., visual-tactile trials minus visual-only trials). First, we inspected and confirmed the presence of the P50 component over central-posterior electrode sites approximately 50 ms after applying tactile taps, a sensory response shown to reflect influx of tactile input into primary SCx (Eimer and Forster, 2003; Hämäläinen et al., 1990).

Then, we proceed to examine the development of the CSD signal from SEPs (VEP-free) by comparing the mean amplitude from contralateral and ipsilateral brain activity in each memory load for both stimulus conditions. First, we analysed the mean amplitudes in the time window of the vdN2CC (200-300 ms). Repeated-measures ANOVA yielded a significant triple interaction between the factors stimulus, hemisphere, and load ($F_{(1,19)}$ = 9.760, P = 0.006). We followed-up this interaction for each type of stimulus, showing that no significant interaction was found when maintaining images of shapes in WM ($F_{(1,19)}$ = 2.474, P = 0.132). In contrast, a significant interaction of hemisphere by load was found when maintaining hand images in WM ($F_{(1,19)}$ = 9.958, P = 0.005). The follow-up tests indicate a significant difference between ipsilateral and contralateral persistent activity only in the high load condition ($t_{(19)}$ = 3.189, P = 0.005; 4.1 *vs.* 0.5; *SEM:* ±1.5 and ±1.2). Similar pattern was found when analysing the vdCDA (300-900ms), specifically, we found a significant triple interaction between the stimulus, hemisphere, and load ($F_{(1,19)}$ = 8.778, P = 0.008). In the shape stimulus condition, the interaction between hemisphere and load yielded a non-

significant difference ($F_{(1,19)}$ = 1.568, P = 0.226), whereas in the hand condition it reached significance ($F_{(1,19)}$ = 12.001, P = 0.003). Lastly, a significant difference between ipsilateral and contralateral persistent activity was found only in the high load condition ($t_{(19)}$ = 3.026, P = 0.007; 0.8 *vs.* -3.2; *SEM:* ±1.1 and ±1.4). Similar analyses were conducted over more frontal and posterior electrode sites. However, the interaction between hemisphere and memory load did not reach significance over more frontal and posterior electrode sites (all *Ps* > 0.130). Taken together, this well-defined persistent activity appeared over parietal electrode sites and increased with the number of hand images to-be-remembered.
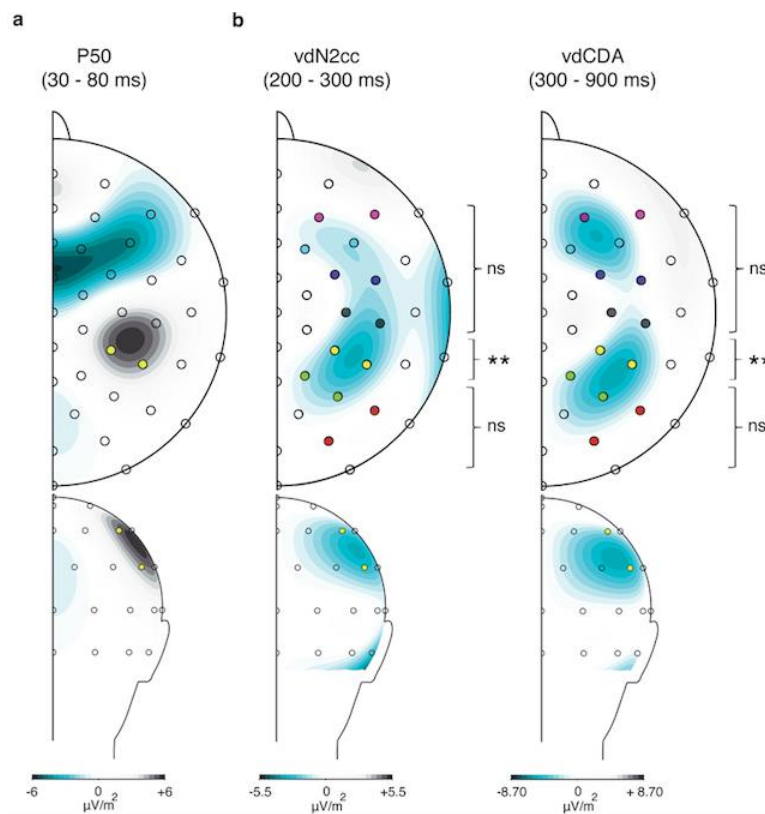

Figure 5. Current source density (CSD) topographical maps SEPS (VEP-free) in the hand stimulus condition. (a) CSD scalp distribution in the P50 time windows after collapsing contralateral and ipsilateral evoked potentials for both memory loads revealed an early positivity over central-parietal electrodes upon arrival of brief tactile probes. (b) The difference of CSD topographies in the vdN2cc and vdCDA components after subtracting ipsilateral activity to contralateral in each memory load and activity from the low memory load to the high load condition. A significant difference between memory loads was only found over parietal electrode sites (CP3/CP4 and CP5/CP6 electrodes of the

10-20 system -in yellow). No significant differences were found over more anterior and posterior scalp regions. **, $P < 0.01$; ns, non-significant, n=20.

Interestingly, a slightly anterior to posterior shift can be observed across time in the CSD topographies (Figure 5). This might reflect the underlying mechanism involved in processing visually acquired bodily information; a process known to elicit activity over posterior parietal brain regions such as secondary somatosensory and associative cortices in studies of action and touch observation, where visuomotor transformation, somatosensory spatial discrimination, and integration of proprioceptive signals seem to play a crucial role (Ebisch et al., 2008; Kuehn et al., 2014; Meyer et al., 2011; Schaefer et al., 2009).

4. Discussion

We present a neural signature of WM beyond visual cortices (namely visually driven CDA; vdCDA) and describe the modulation of SCx's activity during encoding and maintenance of visually perceived body images (i.e. hands) in a visual WM task. Specifically, we found that persistent contralateral activity increased over SCx during the retention interval of the stimuli in WM depending on the number of hand images to-be-remembered. This component is present over and above visual carry over effects and seems to reflect encoding and maintenance of visually perceived body-related information. Interestingly, the modulation by memory load over SCx was not found when maintaining in WM the control non-body-related visual stimuli (i.e., shape images), which in line with previous studies elicited a contralateral delayed activation (CDA) over more posterior electrode sites, suggesting recruitment of visual regions (Vogel et al. 2005; McCollough et al. 2007; Luck and Vogel 2013).

The subtraction of visual-only trials from visual-tactile trials allowed us to dissociate neural responses evoked in SCx during visual processing, over and above a potential superimposition of activity from VEPs. The subtractive method on which this work is based has been previously employed in studies examining multisensory integration (Dell'Acqua et al., 2003; Teder-Sälejärvi et al., 2002). However, only recently it has been used to show

visually driven but visually independent SCx activity (Sel et al. 2014). Moreover, based on previous studies that exploited the contralateral organisation of visual and somatosensory cortices (Vogel and Machizawa 2004; Katus et al. 2014, 2015) we computed parallel subtractions across these sensory regions to examine persistent activity associated with the consolidation of the visual stimuli in the same WM task. This approach allowed us to infer that attentional selection and WM maintenance of body images, as well as the modulation by load in SCx, are not a mere carryover effects from concomitant activation in visual cortices.

4.1. Theoretical implications in the WM framework

Dominant theories in WM postulate that the storage of information occurs in brain areas that also process this information in the absence of WM demands, for instance, in sensory cortex. These approaches converge upon the understanding of WM as a re-establishment of perceptual experience (D'Esposito and Postle, 2015; Postle, 2006; Serences et al., 2009; Tsubomi et al., 2013). The results from the present study contribute to these accounts by showing that visually perceived information can engage distinct sensory cortex during a similar WM task depending on the nature of the information to-be-remembered. In particular, it seems that a re-establishment of perceptual experience is observed in SCx during WM for body-related visual information, engaging here the sensory cortex matching the perceptual features embedded in the stimuli to-be-remembered.

These results are in line with previous work describing neural recruitment contingent to the specific characteristic to-be-remembered within a given stimulus set (Lee et al., 2013; Serences et al., 2009), as well as involvement of particular brain regions during encoding and maintenance of specific stimuli (Gazzaley et al., 2004; Ranganath et al., 2004). In the current study, we compared visually perceived body-related information with comparable non-body information (note that performance in both stimulus conditions was comparable), and attribute our effect over SCx to the recruitment of already established representations of the stimuli to-be-remembered (body part) rather than to mere effects of early visual processing. This is in agreement with previous fMRI work showing increased activity in motor areas

during consolidation of manipulable objects in WM (Mecklinger et al., 2004, 2002) and with the idea revisited by Brady et al. (2016) regarding the importance of long-term associations in shaping the processing of information beyond early perceptual features (Konkle and Brady, 2010; McWeeny et al., 1987).

Further studies would require examining the integration and regulation of different features that may be integrated in bodily percepts (e.g., visual features, depicted kinematics). This integration is likely supported by sensory-specific and domain-general WM mechanisms. A number of publications have reported modulation of neural oscillations, which biophysical underpinnings are better understood than those in the time-domain, in different frequency bands concomitant to the type of stimulus and time course of WM (Roux et al., 2012; Spitzer et al., 2014). Also in the frequency-domain, a recent study has reported domain-general components that correlate with activity in either visual areas or SCx, depending on the content of WM. Interestingly, one of these components is in the form of sustained activity in parietal cortices during the retention interval and test memory phase (van Ede, Jensen, and Maris 2017). We consider that our reported peak of activity over parietal electrode sites in the hand stimulus condition is due to processing of visual body-related information. Examining neural oscillations across different sensory areas and classically recognised top-down cortices (e.g., prefrontal cortex) is a promising avenue in the juxtaposition of the embodiment and WM fields.

4.2. Theoretical implications in the embodiment framework

SCx holds a representation of our own body in the brain (Bolognini et al., 2011; Gazzola and Keysers, 2009; Martuzzi et al., 2014) and its engagement in body and action perception, as well as in higher cognitive tasks such as emotion recognition (Pitcher et al., 2008; Sel et al., 2014) have provided solid grounds for embodiment theories (Gallese and Sinigaglia, 2011). The role of our own body representations in WM has been suggested in early behavioural studies finding that storage of body-related images is impaired by concomitant tasks involving perception and memory encoding of additional body-related

information; conversely, adding non-body-related visuospatial processing did not affect this process (Rumiati and Tessari, 2002; Smyth et al., 1988; Smyth and Pendleton, 1989; Wood, 2007; Wooding and Heil, 1996). In a similar vein, more recent studies indicate that SCx plays an important role in motor learning by observation (Lametti and Watkins, 2016; McGregor et al., 2016). It also seems to represent actions that are visually perceived, resembling activity elicited when touching or being touched (Keysers et al., 2004; Kuehn et al., 2013), but see touch and use of tools in Chan and Baker (2015). These activations may go beyond just perceiving bodies, for example, seeing similar objects with different textures and seeing hands interacting with different objects elicits SCx activity that can be decoded in a content-specific manner (Meyer et al. 2011). Conversely, processing more 'pure visual' properties such as colour did not elicit considerable changes in SCx's activity (Sun et al., 2016). Importantly, our data supports these studies while suggesting new evidence for the role of SCx in encoding and maintaining of body-related images in WM.

In the present study, we speculate that SCx and associated cortices represent body-related stimuli or at least some of the dimensions that represent the percept in WM, and that this process is underpinned by exposition and functional associations between one's experience and others bodies. This repeated perceptual stimulation is likely to be stored as sensory associations between the tactile sensation and the view of bodies (e.g., feeling or moving my own hands and seeing others' hands). To further understand to what extend motor and somatosensory brain areas do not only contribute but are utterly necessary to memory maintenance is still to be understood.

4.3. Conclusion

Previous studies have shown that WM consolidation of arbitrary stimuli that are similar to our control stimuli (i.e. shapes) engages sensory recruitment of visual regions (Todd and Marois, 2004; Tsubomi et al., 2013; Vogel and Machizawa, 2004). Likewise, consolidating tactile information such as vibrations and tactile taps elicits recruitment of SCx (Harris et al., 2002; Katus et al., 2015, 2014). Our results support a more dynamic process whereby recruitment of

sensory areas during WM is not exclusively dictated by the sensory modality used to originally perceive the stimuli-to-remembered. Instead, this process seems moderated by the nature of the information embedded in the percept. In our particular case, SCx responses to visually perceived body-related information probably reflect associations that summon processing resources during WM. The presence of this neural response suggests evidence for encoding of visual information in functionally different sensory cortical regions that match the functional and perceptual characteristics of the perceived stimuli (i.e. body images in SCx).

Author contributions

B.C.-M, A.G-P, A.C and B.F designed the research; A.G-P collected the data; A.G-P, B.C.-M, and B.F. analyzed and interpreted the data; A.G-P and B.C.-M wrote drafts of the manuscript, and A.C, 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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