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2 Manuscript Title

3 **Multiple foci of spatial attention in multimodal working memory**

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19 Keywords: Selective attention, multisensory (touch / vision), working memory (WM), event-
20 related potentials (ERPs)

21 **Abstract**

22 The maintenance of sensory information in working memory (WM) is mediated by the
23 attentional activation of stimulus representations that are stored in perceptual brain regions.
24 Using event-related potentials (ERPs), we measured tactile and visual contralateral delay
25 activity (tCDA / CDA components) in a bimodal WM task to concurrently track the attention-
26 based maintenance of information stored in anatomically segregated (somatosensory and
27 visual) brain areas. Participants received tactile and visual sample stimuli on both sides,
28 and in different blocks, memorized these samples on the same side or on opposite sides.
29 After a retention delay, memory was unpredictably tested for touch or vision. In same side
30 blocks, tCDA and CDA components simultaneously emerged over the same hemisphere,
31 contralateral to the memorized tactile / visual sample set. In opposite side blocks, these two
32 components emerged over different hemispheres, but had the same sizes and onset
33 latencies as in the same side condition. Our results reveal distinct foci of tactile and visual
34 spatial attention that were concurrently maintained on task-relevant stimulus
35 representations in WM. The independence of spatially-specific biasing mechanisms for
36 tactile and visual WM content suggests that multimodal information is stored in distributed
37 perceptual brain areas that are activated through modality-specific processes that can
38 operate simultaneously and largely independently of each other.

39 .

40 **1. Introduction**

41 Information that is no longer physically present, but needed for ongoing behavior, is
42 temporarily stored in working memory (WM). The neural basis of WM involves multimodal
43 brain regions such as prefrontal cortex (PFC, Curtis & D'Esposito, 2003; Fuster &
44 Alexander, 1971; Postle, 2006; Sreenivasan et al., 2014) and posterior parietal cortex

45 (PPC, Xu & Chun, 2006), as well as modality-specific perceptual brain areas (Pasternak &
46 Greenlee, 2005; Supèr et al., 2001; Zhou & Fuster, 1996). According to the sensory
47 recruitment model of WM (Jonides et al., 2005), cortical regions that have encoded sensory
48 signals into WM also mediate the short-term storage of these signals. This hypothesis is
49 supported by fMRI and EEG experiments demonstrating that stimulus-specific WM content
50 can be decoded from neural activity in sensory cortex (Emrich et al., 2013; Harrison &
51 Tong, 2009). Higher-level cortical areas, such as the PFC, which assert top-down influence
52 on perceptual areas are thought to regulate the maintenance of task-relevant stimulus
53 representations in sensory cortex (Awh & Jonides, 2001; Awh et al., 2006; Curtis &
54 D'Esposito, 2003; Postle, 2006; Sreenivasan et al., 2014), but these higher brain regions
55 may also play a role in information storage (Riley & Constantinidis, 2016; Romo & Salinas,
56 2003; Ester et al., 2015; Mendoza-Halliday et al., 2014).

57 The attention-based maintenance of WM representations is thought to be governed
58 by a single supramodal control system that operates across all sensory modalities (Cowan,
59 2011; Cowan et al., 2011). However, this type of supramodal attentional control may be
60 difficult to reconcile with the sensory recruitment model. If the storage of sensory
61 information in working memory is based on the recruitment of perceptual brain areas, the
62 maintenance of this information may also be mediated by modality-specific attentional
63 processes. For example, tactile and visual WM representations have different spatial
64 layouts, because they were encoded into WM by sensory neurons whose receptive fields
65 are organized in a modality-specific fashion (somatotopic versus retinotopic; Katus et al.,
66 2015b; Golomb et al., 2008; Golomb & Kanwisher, 2012). Hence, spatially selective
67 processes that direct focal attention to WM content should rely on such modality-specific
68 coordinate systems, as these index the locus where sensory information is stored in the
69 brain. The top-down attentional control of working memory in different modalities can be

70 investigated in multimodal WM tasks that require the concurrent maintenance of tactile and
71 visual stimuli. In such tasks, distinct foci of tactile and visual spatial attention may emerge
72 simultaneously over somatosensory and visual cortex. However, the hypothesis that
73 spatially selective processes bias modality-specific (tactile/visual) WM representations
74 simultaneously, and perhaps even independently, has so far never been tested empirically.

75 Previous event-related potential (ERP) studies have uncovered distinct
76 electrophysiological correlates of the attention-based maintenance of visual and tactile WM
77 representations. The contralateral delay activity (CDA) emerges during the retention of
78 visual stimuli over posterior visual areas contralateral to the visual field in which memorized
79 items had been presented (Vogel et al., 2005; Vogel & Machizawa, 2004). The CDA is
80 sensitive to WM load and individual differences in WM capacity, and reflects the spatially
81 selective maintenance of information in visual WM. The tactile CDA component (tCDA)
82 shows a similar response profile as its visual counterpart, but has a modality-specific
83 topography over contralateral somatosensory cortex (Katus & Eimer, 2015; Katus et al.,
84 2015a; Katus & Müller, 2016; for further discussion of the relationship between the tCDA
85 and the somatotopic organization of tactile WM, see Katus et al., 2015b). So far, the CDA
86 and tCDA components have been investigated exclusively with unimodal (visual or tactile)
87 WM tasks. For the first time, we here concurrently measured the tCDA and CDA
88 components in a bimodal WM task to track the maintenance of tactile and visual WM
89 representations simultaneously. To distinguish between the tCDA and CDA, we used
90 current source density (CSD) transforms (Tenke & Kayser, 2012), which minimize volume
91 conduction effects between these components. Note that both the tactile and visual CDA
92 are inherently spatially selective markers of WM maintenance, because these lateralized
93 components are isolated by subtracting ipsilateral from contralateral ERPs (as defined
94 relative to the side where stimuli are memorized). We therefore employed a spatial

95 manipulation to examine whether the spatially selective biasing of tactile and visual WM
96 representations is mediated by dissociable processes.

97 Bimodal (tactile/visual) sample sets were simultaneously presented on the left and
98 right sides (Figure 1). Participants memorized the locations of two tactile stimuli and the
99 colors of two visual stimuli, before memory was unpredictably tested for vision or touch. The
100 location where the task-relevant visual and tactile sample stimuli had to be retained
101 alternated across experimental blocks. In half of all blocks, participants memorized tactile
102 and visual stimuli on opposite sides (touch left / vision right, or vice versa). In the other half,
103 their task was to memorize tactile and visual stimuli on the same side. If distinct spatially
104 selective biasing mechanisms maintain focal attention on tactile and visual memory
105 representations, the tCDA and CDA components should emerge over opposite
106 hemispheres in opposite sides blocks, whereas in same sides blocks, both components
107 should manifest over the same hemisphere. The tCDA/CDA components should be
108 statistically reliable (as indexed by amplitudes that differ from zero), and importantly, the
109 polarities of these components should differ between same and opposite sides blocks.
110 Such a pattern of results would strongly support the hypothesis that separate spatially
111 selective biasing mechanisms maintain focal attention on stimulus representations that
112 were encoded into WM through different modalities.

113

114

115 **2. Materials and Methods**

116 **2.1. Participants**

117 Twenty neurologically unimpaired paid adult participants took part in the experiment. One
118 participant was excluded due to poor behavioral performance (memory accuracy for tactile
119 stimuli was below 60%), another because of excessive alpha activity. The remaining

120 eighteen participants (mean age 29 years, range 19-42 years, 11 female, 17 right-handed)
121 all had normal or corrected vision. The study was conducted in accordance with the
122 Declaration of Helsinki, and was approved by the Psychology Ethics Committee, Birkbeck
123 College. All participants gave informed written consent prior to testing.

124

125 **2.2. Stimulation hardware and stimulus materials**

126 Participants were seated in a dimly lit recording chamber with their hands covered from
127 sight. Tactile stimuli were presented by eight mechanical stimulators that were attached to
128 the left and right hands' distal phalanges of the index, middle, ring and small fingers. The
129 stimulators were driven by custom-built amplifiers, controlled by MATLAB routines (The
130 MathWorks, Natick, USA) via an eight-channel sound card (M-Audio, Delta 1010LT). Tactile
131 stimuli were presented in sets of four simultaneous pulses (two to each hand), consisting of
132 100 Hz sinusoids that were presented for 150 ms with an intensity of 0.37 N. Headphones
133 presented continuous white noise to mask any sounds produced by tactile stimulation.

134 Visual stimuli were shown for 150 ms at a viewing distance of 100 cm against a
135 black background on a 22 inch monitor (Samsung SyncMaster 2233; 100 Hz refresh rate,
136 16 ms response time). Four differently colored squares were presented simultaneously (one
137 in each quadrant). Each square had a size of 0.63° of visual angle, and all squares were
138 equidistant from central fixation, with a horizontal eccentricity of 0.64° and a vertical
139 eccentricity of 0.53° of visual angle (measured relative to the squares' centers). Six
140 equiluminant colors (11.8 cd/m^2) were used in the experiment (red, green, blue, yellow,
141 cyan and magenta). A white fixation dot was constantly present on the screen centre
142 throughout the experiment. At the end of each trial, a question mark was shown centrally for
143 2000 ms to indicate the response period.

144

145 **2.3. Stimulation procedure and task**

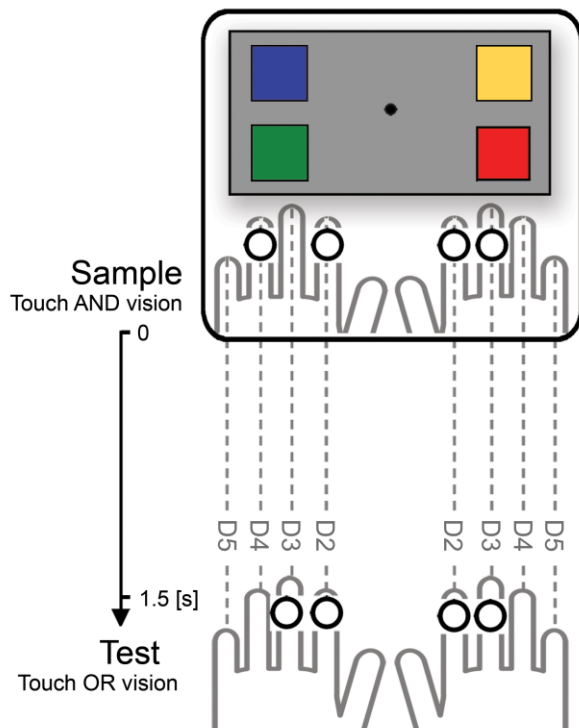
146 We used a bimodal WM procedure that combined two lateralized change detection
147 tasks for tactile and visual stimuli. Figure 1 illustrates the stimulation procedure. Bimodal
148 (tactile and visual) sample sets were followed after 1500 ms by a unimodal test set (tactile
149 or visual, 50%). The sample sets included two visual stimulus pairs on the left and right side
150 of the monitor, and two tactile stimulus pairs, presented simultaneously to the left and right
151 hands. Participants were instructed to memorize visual and tactile stimulus pairs on one
152 task-relevant side, and to decide whether the (tactile or visual) test stimulus set matched
153 the memorized sample set on the respective task-relevant side. In different blocks, tactile
154 and visual stimuli had to be retained on the *same side* (e.g., memorize visual stimuli on the
155 left side, and tactile stimuli on the left hand), or on *opposite sides* (e.g., visual stimuli on the
156 left side and tactile stimuli on the right hand).

157 On each trial, two stimulators were randomly and independently selected on each
158 hand to deliver the tactile sample pulses. On those trials where memory was tested for
159 touch after the retention period, the locations of the tactile test stimulus set on the task-
160 relevant hand were either identical to the sample set's locations (match trials, 50%) or
161 differed (mismatch trials, 50%). In two thirds of all mismatch trials, test stimulus pairs were
162 delivered to one previously stimulated location and one new location (where no sample had
163 been presented). In the remaining third of mismatch trials, both test stimuli were presented
164 to new locations. On the task-irrelevant hand, test stimuli were also presented at matching
165 or mismatching locations, independent of whether there was a match or mismatch on the
166 task-relevant hand. Visual sample sets consisted of two squares on the left side and two
167 squares on the right side in four randomly selected colors. On those trials where visual
168 memory was tested, the visual test set was either identical to the sample set on the task-
169 relevant side (match trials, 50%) or differed (mismatch, 50%). In two thirds of all mismatch

170 trials, one of the two colors changed across sample and test. In the remaining third of
171 mismatch trials, the task-relevant colored squares in the sample set swapped their locations
172 in the test set. Visual test stimuli on the task-irrelevant side could also match or mismatch
173 the sample set on this side, independently of whether there was a match or mismatch on
174 the relevant side.

175 Since memory was unpredictably tested for touch or vision, participants had to
176 memorize task-relevant tactile and visual stimuli on each trial. They signalled a match or
177 mismatch between sample and test on the relevant hand / side with a vocal response (“a”
178 for match and “e” for mismatch) that was recorded with a headset microphone. A question
179 mark shown on the monitor for 2000 ms indicated the response period, which started 360
180 ms after test stimulus onset. The interval between the end of the response period and the
181 start of the next trial varied between 720 and 980 ms (average 850 ms). The experiment
182 involved 528 trials, presented during twelve blocks with 44 trials each. The relevant side for
183 the visual task changed after every three blocks, and the relevant side for the tactile task
184 after six blocks. Task instructions specifying the relevant locations for the visual and tactile
185 tasks were shown on the monitor prior to the start of each block. Participants were asked to
186 avoid head and arm movements, to maintain central gaze fixation, and to prioritize accuracy
187 over speed. Feedback on hit and correct rejection rates was provided after each block. Half
188 of the participants performed the same side condition during the first three blocks and
189 during the last three blocks of the experiment. The remaining participants performed the
190 opposite side condition during these blocks (and the same side condition in blocks four to
191 nine). Before the experiment, participants completed training blocks of 25 trials for the same
192 side as well as opposite sides condition.

193



194

195 **Figure 1. Stimulation procedure and task.** A bimodal (tactile-visual) sample set was
 196 followed after 1.5 s by a unimodal test set (unpredictably tactile or visual). The locations of
 197 the tactile sample stimuli (indicated by circles) were memorized on one task-relevant hand
 198 (left or right), and the colors of the visual stimuli were memorized in one visual field (left or
 199 right). In *same side* blocks, tactile and visual sample stimuli were memorized on the same
 200 side. In *opposite side* blocks, participants memorized tactile samples on the left hand and
 201 visual samples on the right side, or vice versa. In each trial participants reported a match or
 202 mismatch between sample and test sets (on the task-relevant hand/side).

203

204 **2.4. Analysis of EEG data**

205 EEG data, sampled at 500 Hz using a BrainVision amplifier, were DC-recorded from 64
 206 Ag/AgCl active electrodes at standard locations of the extended 10-20 system. Two
 207 electrodes at the outer canthi of the eyes monitored lateral eye movements (horizontal
 208 electrooculogram, HEOG). Continuous EEG data were referenced to the left mastoid during

209 recording, and were offline re-referenced to the arithmetic mean of both mastoids. Data
210 were submitted to a 30 Hz low-pass finite impulse response filter (Blackman window, filter
211 order 500). Epochs were extracted for the 1500 ms interval after presentation of the sample
212 sets, and were corrected relative to 200 ms pre-stimulus baselines.

213 Blind source separation of EEG data was performed using the independent
214 component analysis (ICA) algorithm implemented in the EEGLab toolbox (Delorme &
215 Makeig, 2004; Delorme et al., 2007). Independent components (ICs) accounting for eye
216 blinks were subtracted from the data. Epochs with lateral eye movements were identified
217 and rejected using a differential step function that ran on the bipolarized HEOG (step width
218 100 ms, threshold 30 μ V). After exclusion of trials with saccades, we additionally subtracted
219 ICs accounting for horizontal eye movements, to remove residual traces of ocular artifacts
220 that had not exceeded the amplitude threshold of the step function. Because slow
221 lateralized drifts caused by head or body movements can compromise the analysis of
222 sustained lateralized ERP components, epochs with such drifts were identified and rejected
223 in two steps. First, 27 difference waves were computed per trial by calculating the
224 difference between ERPs at corresponding left- and right-hemispheric electrodes (e.g., C3
225 minus C4) within the time window used for the subsequent ERP analyses (300-1500 ms
226 after sample onset). Epochs that contained difference values exceeding a threshold of +/-
227 50 μ V were rejected. In a second step, we converted single-trial EEG data to current source
228 densities (CSDs) before calculating difference waves for the 27 lateral electrode pairs.
229 Difference values in the time window of interest (300-1500 ms) were standardized across
230 trials via z-transformations. Trials in which at least two electrode pairs showed z-scores
231 exceeding a threshold of +/- 3 were rejected. Note that this procedure was only used to
232 identify epochs with artifacts - the z-scores obtained from CSD-transformed data were not
233 used for statistical analysis. All remaining EEG epochs were submitted to *Fully Automated*

234 *Statistical Thresholding for EEG Artifact Rejection* (FASTER, Nolan et al., 2010), and were
235 subsequently converted to CSDs (iterations = 50, m = 4, lambda = 10^{-5} ; see Tenke &
236 Kayser, 2012) to minimize effects of volume conduction between the tCDA and CDA
237 components. After artifact rejection, 91.4% of all epochs remained for statistical analysis
238 (same side: 91.5%; opposite sides: 91.3%). These epochs were averaged separately for
239 same side and opposite sides blocks.

240 EEG data from pairs of three adjacent electrodes were averaged, separately for the
241 hemisphere contralateral and ipsilateral to the currently relevant side for the visual and
242 tactile tasks. Tactile contralateral delay activity (tCDA component) was measured at lateral
243 central scalp regions (C3/4, FC3/4, CP3/4). Visual contralateral delay activity (CDA) was
244 measured at lateral occipital scalp regions (PO7/8, PO3/4, O1/2). Statistical analyses were
245 conducted on CSD amplitudes averaged between 300 ms and 1500 ms relative to sample
246 onset (cf., Katus et al., 2015a).

247 Error bars in graphs showing contra- / ipsilateral difference values indicate 95%
248 confidence intervals, which were calculated for each condition by t-tests against zero (i.e.,
249 no lateralized effect). Statistical significance of difference values is marked by error bars (or
250 colored shadings in CSD plots) that do not overlap with the zero axis (i.e., $y \neq 0$).
251 Topographic voltage maps display spline-interpolated difference values that were obtained
252 by subtracting CSDs ipsilateral to the visual task from contralateral CSDs. The resulting
253 difference values were mirrored to the opposite hemisphere, to obtain symmetrical but
254 inverse voltage values for both hemispheres. As data in these maps are aligned to illustrate
255 lateralized effects for visual sample stimuli that are memorized on the right side, these
256 maps differ as to whether tactile sample stimuli are memorized on the right hand (same
257 side condition) versus left hand (opposite sides condition).

258

259 **2.5. Statistical analyses**

260 The F- and t-statistics reported in the manuscript were obtained from repeated measures
261 ANOVAs and t-tests. Effect sizes are quantified by partial eta² values (η^2_p) in ANOVAs and
262 by Cohen's d in t-tests. For the jackknife-based procedure (Miller et al., 1998) employed to
263 compare onset latencies of the tCDA and CDA components between same side and
264 opposite sides blocks, we used one-way ANOVAs, with corrected F- and partial eta² values
265 ($F_{\text{corrected}}$, $\eta^2_{p\text{corrected}}$), according to Miller et al., 1998 and Ulrich & Miller, 2001.

266 Because non-significant effects cannot be easily interpreted in the context of
267 conventional null-hypothesis significance testing, we additionally calculated Bayes factors
268 (Wagenmakers et al., 2010; Rouder et al., 2012; Rouder et al., 2009) using the software
269 JASP (JASP team, 2016). The Bayes factor for the null-hypothesis (BF_{01}) denotes the
270 relative evidence in the data supporting the null-hypothesis, as compared with the
271 alternative hypothesis, and corresponds to the inverse of the Bayes factor for the alternative
272 hypothesis (BF_{10}). Depending on whether an effect was statistically significant or non-
273 significant, we here report the Bayes factor for the alternative (BF_{10}) or null-hypothesis
274 (BF_{01}), respectively. Reliable evidence for either hypothesis is indexed by a $BF > 3$
275 (Jeffreys, 1961), suggesting that the empirical data is at least 3 times more likely under this
276 hypothesis as compared with the competing hypothesis.

277

278 **3. Results**

279 **3.1. Behavioral performance**

280 Participants responded correctly on 91.1% of all trials. The percentage of correct responses
281 and mean reaction times (RTs) were virtually identical in same side and opposite sides
282 blocks (91.0% versus 91.1%; 871 ms versus 863 ms). Full factorial ANOVAs examined
283 whether RTs and memory accuracy (d') were influenced by the factors *attended sides*

284 (same vs. opposite) and *tested modality* (touch vs. vision). RTs were significantly faster on
285 trials in which visual WM was tested (815 ms versus 918 ms when touch was tested; $F(1,$
286 $17) = 23.091$, $p < 0.001$, $\eta^2_p = 0.576$, $BF_{10} = 180.959$), but accuracy was not significantly
287 increased on these trials ($d' = 3.2$ versus 2.8 ; $F(1, 17) = 3.347$, $p = 0.085$, $\eta^2_p = 0.164$, BF_{01}
288 $= 1.040$). The factor *attended sides* did neither influence RTs ($F(1, 17) = 0.463$, $p = 0.505$,
289 $\eta^2_p = 0.027$, $BF_{01} = 3.350$) nor memory accuracy ($F(1, 17) = 0.220$, $p = 0.645$, $\eta^2_p = 0.013$,
290 $BF_{01} = 3.729$), and no significant interactions were found between *attended sides* and
291 *tested modality* (RTs: $F(1, 17) = 1.280$, $p = 0.274$, $\eta^2_p = 0.070$, $BF_{01} = 2.362$; Accuracy: $F(1,$
292 $17) = 0.001$, $p = 0.971$, $\eta^2_p = 0.000$, $BF_{01} = 4.112$).

293

294 **3.2. Event-related potentials**

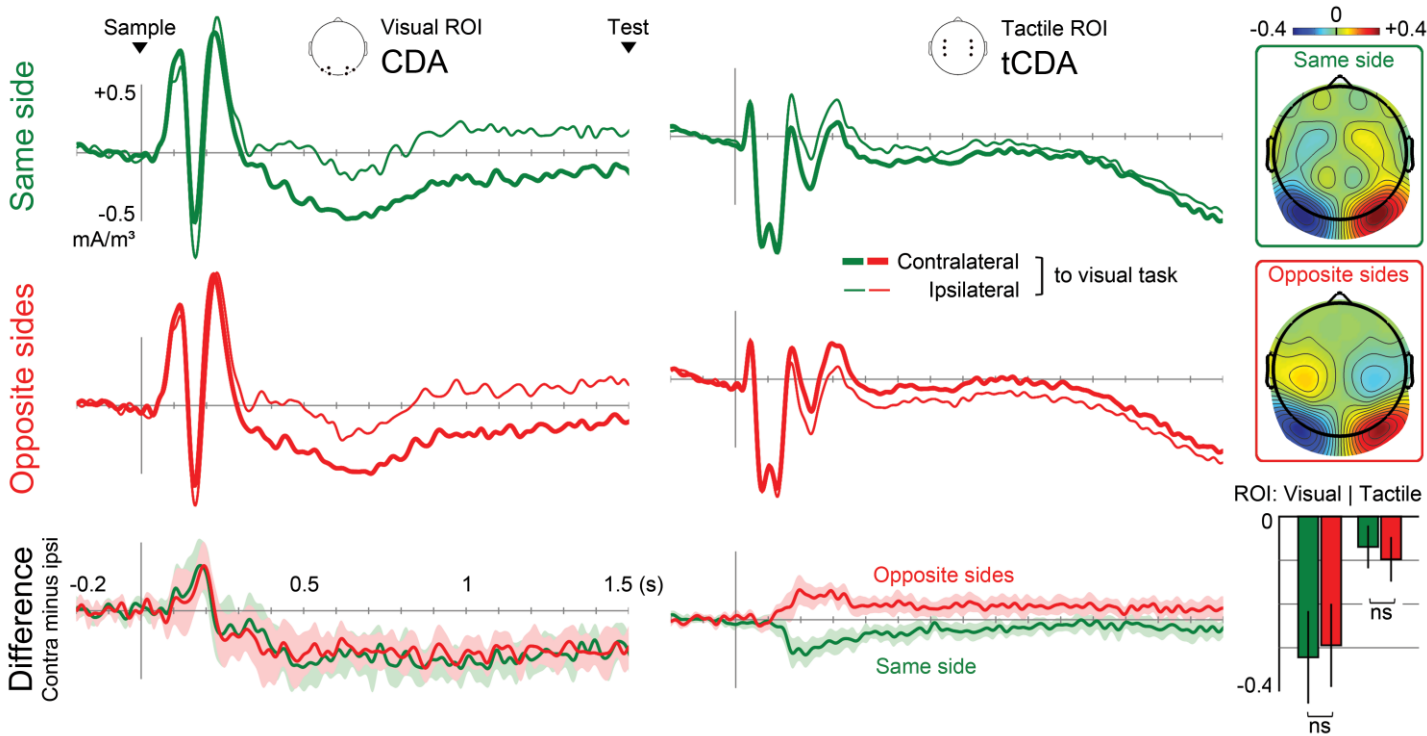
295 Lateralized effects were present in CSDs recorded at visual and somatosensory regions of
296 interest (ROIs), both in same side and opposite sides blocks; see Figure 2. The visual CDA
297 component was found contralateral to the side where visual stimuli were memorized. The
298 polarity of the somatosensory tCDA component (defined relative to the task-relevant side
299 for the visual task) reversed between blocks where both tasks were performed on the same
300 side as opposed to opposite sides. This tCDA polarity reversal is displayed in the CSDs and
301 difference waves in Figure 2, as well as in the topographical maps, which show tCDA and
302 CDA components over lateral central and posterior regions of the same hemisphere in
303 same side blocks, and over opposite hemispheres in opposite sides blocks.

304 Statistical analyses were conducted on CSD amplitudes that were averaged for the
305 time period between 300 and 1500 ms after the sample set. A three-way repeated
306 measures ANOVA with the factors *attended sides*, *ROI* and *contralaterality* (now defined
307 independently for tactile and visual ROIs relative to the task-relevant hand and the task-

308 relevant visual field, respectively) assessed contralateral and ipsilateral CSDs at
309 somatosensory and visual ROIs in same side and opposite sides blocks. Contralateral CSD
310 amplitudes were more negative than CSDs measured ipsilateral to the task-relevant hand /
311 side, as reflected by a significant main effect of contralaterality ($F(1, 17) = 58.782, p < 10^{-6},$
312 $\eta^2_p = 0.776, BF_{10} > 10^4$). Lateralized effects were more pronounced over visual as
313 compared to tactile ROIs (contralaterality x ROI interaction: $F(1,17) = 29.949, p < 10^{-4}, \eta^2_p =$
314 $0.638, BF_{10} = 619.679$), and this result suggests that the visual CDA component was larger
315 in size than its somatosensory counterpart. No further main effects or interactions were
316 statistically significant (all p s > 0.1). Note that the absence of a significant interaction
317 between the factors contralaterality and attended sides ($F(1, 17) = 0.000, p = .984, \eta^2_p =$
318 $0.000, BF_{01} = 4.114$) implies that tCDA and CDA components had similar sizes in blocks of
319 the same side and opposite sides conditions (see bar graphs in Figure 2). Importantly, t -
320 tests against zero confirmed that the simultaneously elicited tCDA / CDA components were
321 statistically reliable in same side blocks (tCDA: $t(17) = 3.117, p = 0.006, d = 0.735, BF_{10} =$
322 7.796 ; CDA: $t(17) = 6.527, p < 10^{-4}, d = 1.538, BF_{10} > 10^3$), as well as in opposite sides
323 blocks (tCDA: $t(17) = 4.211, p = 0.001, d = 0.992, BF_{10} = 59.313$; CDA: $t(17) = 6.668, p <$
324 $10^{-4}, d = 1.572, BF_{10} > 10^3$). The difference waveforms in Figure 2 suggest that there were
325 no systematic differences in the onset of lateralized components over somatosensory and
326 visual cortex between same side and opposite sides blocks. To test this formally, we
327 submitted contra-/ipsilateral difference waveforms to a jackknife-based procedure (Miller et
328 al., 1998). Onset latencies were defined as the point in time where amplitudes of tCDA and
329 CDA difference waveforms exceeded an absolute criterion of -0.1 mA/m^3 . There were no
330 significant differences of tCDA / CDA onset latencies between same side and opposite
331 sides blocks (tCDA: $F_{\text{corrected}}(1, 17) = 0.371, p = 0.551, \eta^2_{p\text{corrected}} = 0.021, BF_{01} = 3.489$;
332 CDA: $F_{\text{corrected}}(1, 17) = 0.368, p = 0.552, \eta^2_{p\text{corrected}} = 0.021, BF_{01} = 3.494$), indicating that

333 WM maintenance was not delayed when tactile and visual samples were memorized on
334 opposite sides.

335



336

337 **Figure 2. Lateralized delay activity.** Grand mean CSD-transformed ERPs evoked by the
338 bimodal sample set in blocks where tactile and visual stimuli were memorized on the same
339 side (green) and on opposite sides (red). Results are shown for lateral visual (CDA
340 component) and somatosensory (tCDA component) regions of interest (ROIs). Contralateral
341 and ipsilateral electrodes (thick versus thin lines) were defined relative to the task-relevant
342 side for the visual WM task. The bottom panel shows contra- minus ipsilateral difference
343 waveforms. Shaded areas represent 95% confidence intervals (CIs) for tests of difference
344 values against zero (i.e. no lateralized effect). Topographical maps show the scalp
345 distribution of spline-interpolated difference values obtained by subtracting ipsilateral from
346 contralateral mean amplitude values between 300 - 1500 ms after sample onset. Notably,
347 tCDA and CDA components were triggered over the same hemisphere in same side blocks,

348 and over opposite hemispheres in opposite sides blocks. Bar graphs (bottom right) show
349 mean amplitudes of lateralized components between 300 and 1500 ms after sample onset
350 for visual and somatosensory ROIs, in same side (green) and opposite sides (red) blocks,
351 with laterality now defined relative to the task-relevant side in each task (i.e. relative to the
352 visual task for visual ROIs, and tactile task for tactile ROIs). Statistically reliable lateralized
353 effects are marked by error bars that do not overlap the zero line ($y \neq 0$).

354

355 **3.3. Behavioral control experiment**

356 The absence of behavioral costs in opposite sides relative to same sides blocks in the main
357 experiment may indicate that the demands of the task were too low. This could have
358 resulted in ceiling effects that may have obscured potential performance costs when tactile
359 and visual stimuli had to be maintained on opposite sides. To assess this possibility, we
360 conducted an additional behavioral control experiment that used the same procedures as
361 the main experiment, except that visual WM load was doubled from 2 to 4. Thus,
362 participants had to memorize 6 simultaneously presented stimuli (2 tactile plus 4 visual
363 stimuli), exceeding the suggested WM capacity limit of 4 items (Cowan, 2001), which is
364 assumed to apply even when these items are encoded through different sensory modalities
365 (Cowan, 2011).

366 On each side of the monitor, two visual stimuli that appeared at the same locations
367 as in the main experiment (horizontal and vertical eccentricity relative to the fixation cross:
368 0.64° and 0.53° of visual angle) were accompanied by two additional stimuli (horizontal and
369 vertical eccentricity: 1.17° and 0.53°). In visual mismatch trials, one randomly selected
370 sample stimulus changed its color at memory test. Memory was again unpredictably tested

371 for touch or vision (50% each), and memory matches and mismatches (50% each) were
372 equally likely for the task-relevant and -irrelevant sides.

373 13 volunteers participated in the control experiment. One participant was excluded
374 due to chance performance in the tactile task. The remaining 12 participants (mean age 30
375 years, range 21-42 years, 6 female, 9 right-handed) responded correctly on 85.3% of all
376 trials (tactile task: 90.8% correct, visual task: 79.9% correct). Importantly, and analogous to
377 the main experiment, accuracy was not impaired in opposite sides blocks (opposite vs.
378 same sides: 85.8% vs. 84.9% correct). A formal ANOVA tested memory accuracy (d') for
379 the factors *attended sides* (same vs. opposite) and *tested modality* (touch vs. vision). This
380 analysis confirmed that memory performance did not differ in same sides and opposite
381 sides blocks (*attended sides*: $F(1, 11) = 0.194$, $p = 0.668$, $BF_{01} = 3.199$). Accuracy was
382 higher for the tactile as compared to visual task (*tested modality*: $F(1, 11) = 16.823$, $p =$
383 0.002 , $BF_{10} = 24.940$), but there was no reliable interaction (*attended sides x tested*
384 *modality*: $F(1, 11) = 0.503$, $p = 0.493$, $BF_{01} = 2.290$).

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386

387 **4. Discussion**

388 The current experiment has demonstrated for the first time that the attentional activation of
389 information stored in somatosensory and visual brain areas is mediated by distinct spatially
390 selective processes. Observers simultaneously maintained task-relevant visual and tactile
391 sample stimuli for a subsequent comparison with a test stimulus set. The concurrent
392 attentional maintenance of tactile and visual WM representations was reflected by
393 lateralized tCDA and CDA components with modality-specific topographies. When
394 observers memorized tactile and visual stimuli on the same side, statistically reliable tCDA

395 and CDA components emerged over somatosensory and visual cortex within the same
396 hemisphere, contralateral to the task-relevant stimuli. This finding shows that tactile and
397 visual WM representations can be activated simultaneously in anatomically segregated
398 brain regions, and demonstrates the feasibility of our concurrent tCDA/CDA measurement
399 approach. Even stronger evidence for a dissociation between tactile and visual WM
400 maintenance processes was obtained when tactile and visual stimuli were memorized on
401 opposite sides, resulting in tCDA and CDA components that were simultaneously elicited
402 over different hemispheres (see topographical maps in Figure 2). This result reveals distinct
403 foci of tactile and visual spatial attention, and leads to the conclusion that spatial attention
404 operates in a modality-specific fashion during the maintenance of multimodal WM
405 representations. In spite of the reversed polarity of the tCDA and CDA components in
406 opposite side blocks, their absolute amplitudes and onset latencies did not differ between
407 opposite sides and same side blocks. This observation further bolsters the interpretation
408 that the spatially selective activation of tactile and visual information is mediated by
409 separate modality-specific processes which operate within the same perceptual systems
410 that have accomplished the storage of information in WM.

411 Lateralized ERP components elicited during the delay period of WM tasks mark the
412 spatially selective allocation of attention to WM representations that are stored in perceptual
413 brain regions. Top-down control signals generated in multimodal areas, such as PFC and/or
414 PPC, regulate the maintenance of information in WM by biasing neural activity in sensory
415 cortex in a task-dependent fashion (Curtis & D'Esposito, 2003; Jonides et al., 2005; Postle,
416 2006; Sreenivasan et al., 2014). When behavioral goals change, sensory cortex exhibits
417 corresponding changes in neural activity (Lepsien & Nobre, 2006; Katus et al., 2015b),
418 suggesting that the activation of WM content can be flexibly modulated through the
419 selective allocation of attention to currently task-relevant representations in perceptual brain

420 areas. It has previously been argued that the focus of attention in WM is controlled by a
421 single central / supramodal system that is shared with perception, and also shared between
422 sensory modalities (Cowan, 2011). If this supramodal mechanism operates in a space-
423 based fashion, directing attention to tactile and visual WM representations on opposite
424 sides should lead to costs in behavioral and EEG measures (see evidence from perception
425 research: e.g., Eimer, 2001). However, tCDA and CDA components were neither
426 attenuated nor delayed in opposite sides blocks relative to same side blocks, and WM
427 accuracy was virtually identical in both types of blocks. The absence of any costs for WM
428 performance in opposite sides blocks could have been a result of the bimodal WM task not
429 being sufficiently demanding in the main experiment. In a behavioural follow-up experiment
430 where six stimuli (two tactile and four visual stimuli) had to be simultaneously maintained,
431 performance was again identical in same side and opposite sides blocks (see section 3.3),
432 thereby ruling out this possibility. Overall, these results suggest that the spatially selective
433 allocation of attention to multimodal WM representations is mediated by independent
434 processes for tactile and visual information.

435 To demonstrate the spatial independence of maintenance processes for tactile and
436 visual information, we here used a spatial manipulation, and focused on spatially-selective
437 markers of WM maintenance. We showed that the polarities of the sustained tCDA / CDA
438 components can vary independently of each other, suggesting that these components index
439 modality-specific spatial biasing processes that operate concurrently and independently.
440 However, this conclusion does not necessarily imply that tactile and visual WM rely on
441 independent resources, which would entail independent capacity limitations. To confirm an
442 independence of WM resources for touch and vision, what has to be shown is that the
443 number of items that can be successfully retained in one modality is not affected by the
444 number of items maintained in another modality. Future behavioral and electrophysiological

445 studies hence need to manipulate WM load separately for each modality, with multisensory
446 sample sets sizes that exceed the capacity limits of unimodal WM (cf. Cowan, 2001; Vogel
447 & Machizawa, 2004). Further, while we here employed the lateralized tCDA / CDA
448 components to track the focus of spatial attention in multimodal WM, we do not claim that
449 spatial attention is the only mechanism involved in the activation of WM representations.
450 Attentional mechanisms that operate in a feature- and/or object-based manner may also
451 contribute to the maintenance of information in WM. Recent evidence has linked the visual
452 CDA component with object-based attentional mechanisms (Luria & Vogel, 2011; Ikkai et
453 al., 2010), and it is possible that such mechanisms were also activated in our study, in
454 particular, because the visual task required memory for features (i.e., colors) at specific
455 locations. To shed light on the roles of feature- or object-based attention mechanisms for
456 the maintenance of multimodal information in WM, future experiments could separately
457 manipulate the type of information maintained in touch and vision, and compare tCDA /
458 CDA amplitudes between purely spatial WM tasks and tasks that require WM for features or
459 objects. The novel finding in this study is that spatial attention operates in a modality-
460 specific fashion during WM maintenance. The importance of this finding is owed to the fact
461 that WM representations are inherently spatially specific. Stimulus locations are obligatorily
462 stored in tactile (Katus et al., 2012) and visual WM (Kuo et al., 2009), even for tasks that do
463 not explicitly require memory for locations. The spatial layout of WM representations is a
464 direct consequence of the map-like organization of sensory cortical regions that were
465 recruited to store information (Franconeri et al., 2013; Cavanagh et al., 2010). Spatially
466 selective mechanisms play a vital role in maintaining focal attention on WM content,
467 because this content needs to be activated at the site where it is stored in the brain.

468 The apparent independence of spatial biasing mechanisms for visual and tactile WM
469 may seem inconsistent with previous behavioral and ERP experiments that investigated

470 crossmodal links in perceptual attention (Spence & Driver, 1996; Spence et al., 2000;
471 Eimer, 2001; Eimer & Driver, 2000; Eimer & Schröger, 1998). Directing spatial attention to
472 one side in a primary modality resulted in a corresponding spatial bias for a different
473 secondary modality, even when stimuli in this secondary modality were task-irrelevant or
474 equally likely to appear on either side. It remains possible to deploy auditory and visual
475 attention simultaneously to opposite sides, though not as effectively as directing attention to
476 the same side in both modalities (Spence & Driver, 1996; Eimer, 2001), suggesting that the
477 control mechanisms responsible for allocating spatial attention to sensory stimuli in different
478 modalities are separable but linked. The presence of such crossmodal links has been
479 explained by assuming that perceptual attention operates within a spatial reference frame
480 that is shared across modalities, and is based on external spatial coordinates (Driver &
481 Spence, 1998; Eimer et al., 2001; Eimer & Driver, 2001; for further discussion, see Heed et
482 al., 2015). If spatial synergies in crossmodal perceptual attention are the result of a shared
483 reference frame, the absence of crossmodal interactions during the spatially selective
484 attentional maintenance of visual and tactile WM representations in our study is not
485 surprising, because these representations use different spatial coordinate systems. Stimuli
486 in tactile WM are indexed in somatotopic, rather than allocentric / retinotopic coordinates,
487 as demonstrated by the observation that tCDA components emerge over somatosensory
488 cortex contralateral to the hand where a tactile stimulus is memorized, regardless of
489 whether this hand is placed on the left or right side in external space (Katus et al., 2015b).
490 The incommensurability of spatial coordinate systems for tactile and visual WM
491 representations (somatotopic versus retinotopic) may be the main reason why distinct foci
492 of spatial attention can be simultaneously maintained on multimodal WM content.

493 How might these modality-specific spatial biasing mechanisms for tactile and visual
494 WM contents be implemented at the neural level? There are extensive reciprocal

495 connections between higher-order control regions such as PFC and/or PPC and tactile and
496 visual cortical areas (Andersen et al., 1997; Barbas, 2000). In these control regions,
497 persistent activity of neurons with receptive fields that match the locations of memorized
498 stimuli during WM retention may represent stable activation patterns that are centred on
499 task-relevant coordinates in spatial priority maps (Compte et al., 2000; Wang, 2001; Ikkai &
500 Curtis, 2011; Jerde & Curtis, 2013). The PPC is a zone of multisensory convergence that
501 plays a central role in coordinate transformations, such as the remapping of tactile stimuli
502 into an external, supramodal, frame of reference (Azañón et al., 2010), but it is still
503 controversial whether spatial maps in PPC are consistently referenced to external space
504 (Silver & Kastner, 2009; Medendorp et al., 2011). Neurons in ventral intraparietal area (VIP)
505 of macaque cortex encode stimuli using a variety of modality-specific and intermediate
506 frames of reference (Avillac et al., 2005). These spatial maps may provide pointers to visual
507 and tactile WM representations that employ different modality-specific coordinate systems
508 (cf. Cavanagh et al., 2010). We hypothesize that the spatially selective maintenance of
509 visual and tactile WM representations, as reflected by lateralized delay activity, is mediated
510 by modality-specific mechanisms that bridge the gap between top-down control areas such
511 as PFC and/or PPC, and WM storage systems in sensory cortex. More precisely, we
512 suggest that the recruitment of modality-specific cortical regions for the storage of
513 information is accompanied by a recruitment of modality-specific functions that implement
514 the attentional biasing of WM content at the site where this information is stored in the
515 brain. This interpretation does not rule out the possibility of genuinely supramodal control
516 functions at central levels. For example, connectionist models (e.g., Fuster, 2009) assume
517 that central and modality-specific mechanisms are both critical for WM, which depends on
518 the interplay between executive networks (in frontal cortex) and sensory networks (in
519 posterior cortex). The assumption that modality-specific mechanisms are implicated in WM

520 is further consistent with hierarchical theories, which posit that WM encompasses modality-
521 specific processing systems that are controlled by a central mechanism in a top-down
522 fashion (e.g., Baddeley, 2003).

523

524 **Conclusion** WM emerges due to the attentional activation of brain regions that store
525 stimulus-specific information. We observed distinct foci of tactile and visual spatial attention
526 during the concurrent maintenance of multimodal stimuli in WM. This suggests that
527 multimodal WM representations are stored in distributed brain regions which are subject to
528 separate spatially-specific biasing mechanisms that operate simultaneously and
529 independently during WM retention.

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