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Katus, Tobias and Grubert, Anna and Eimer, Martin (2015) Electrophysiological evidence for a sensory recruitment model of somatosensory working memory. *Cerebral Cortex* 25 (12), pp. 4697-4703. ISSN 1047-3211.

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1 *Full Manuscript Title*

2 **Electrophysiological evidence for a sensory recruitment model of**
3 **somatosensory working memory**

4

5 *Running Title*

6 **Sensory recruitment in tactile working memory**

7

8 *Authors and Affiliations:* Tobias Katus^a, Anna Grubert^a & Martin Eimer^a

9 ^aDepartment of Psychology, Birkbeck College, University of London, London
10 WC1E 7HX, United Kingdom.

11

12 *Corresponding Author:* Tobias Katus

13 Dept. of Psychological Sciences, Birkbeck College, University of London

14 Malet Street, London WC1E 7HX

15 Phone: +44(0)20 7631 6522, Email: t.katus@bbk.ac.uk

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19 *Conflict of Interest:* The authors declare no competing financial interests.

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23 Abstract

24 Sensory recruitment models of working memory assume that information
25 storage is mediated by the same cortical areas that are responsible for the perceptual
26 processing of sensory signals. To test this assumption, we measured somatosensory
27 event-related brain potentials (ERPs) during a tactile delayed match-to-sample task.
28 Participants memorized a tactile sample set at one task-relevant hand to compare it
29 with a subsequent test set on the same hand. During the retention period, a
30 sustained negativity (tactile contralateral delay activity, tCDA) was elicited over
31 primary somatosensory cortex contralateral to the relevant hand. The amplitude of
32 this component increased with memory load and was sensitive to individual
33 limitations in memory capacity, suggesting that the tCDA reflects the maintenance of
34 tactile information in somatosensory working memory. The tCDA was preceded by a
35 transient negativity (N2cc component) with a similar contralateral scalp distribution,
36 which is likely to reflect selection of task-relevant tactile stimuli at the encoding stage.
37 The temporal sequence of N2cc and tCDA components mirrors previous
38 observations from ERP studies of working memory in vision. The finding that the
39 sustained somatosensory delay period activity varies as a function of memory load
40 supports a sensory recruitment model for spatial working memory in touch.

41

42

43 Introduction

44 Working memory (WM) is responsible for the active maintenance of
45 information that is no longer perceptually present. Visual and tactile working memory
46 are both assumed to be based on distributed neural networks that include prefrontal

47 cortex (PFC) and modality-specific perceptual areas. The activation of PFC during
48 the maintenance of visual and tactile stimuli in working memory is well established
49 (Curtis and D'Esposito 2003; Curtis, Rao, D'Esposito 2004; Fuster and Alexander
50 1971; Kostopoulos, Albanese, Petrides 2007; Romo and Salinas 2003; Postle 2005).
51 Additionally, modality-specific visual (Harrison and Tong 2009; Supèr, Spekreijse,
52 Lamme 2001) or somatosensory areas (e.g., Kaas et al. 2013; Zhou and Fuster
53 1996) show persistent activation during the retention of visual or tactile stimuli.
54 Although the exact role of this delay-period activity in visual areas during working
55 memory maintenance and their link to selective visual attention are still debated (e.g.,
56 van Dijk et al. 2010; Lewis-Peacock et al. 2012; Postle et al. 2013), its existence has
57 led to the “sensory recruitment” model of working memory (D'Esposito 2007; Harrison
58 and Tong 2009; Pasternak and Greenlee 2005; Postle 2006). This model postulates
59 that perceptual brain regions which are responsible for the sensory processing of
60 visual or tactile stimuli are also involved in working memory storage. The sustained
61 activation of perceptual areas might be particularly important when working memory
62 tasks require the maintenance of detailed sensory information (e.g., Lee, Kravitz,
63 Baker 2013; see also Sreenivasan, Curtis, D'Esposito 2014).

64 Support for the sensory recruitment model comes from ERP studies of visual
65 working memory (e.g., Vogel, McCollough, Machizawa 2005; Vogel and Machizawa
66 2004). In these studies, bilateral sample displays were followed after a retention
67 interval by test displays, and participants had to match sample and test objects on
68 one side of these displays. A sustained negativity at posterior electrodes contralateral
69 to the side of the memorized objects (contralateral delay activity, CDA) started 300
70 ms after sample onset and persisted throughout the retention interval. The fact that
71 this CDA component is sensitive to manipulations of visual working memory load and
72 to individual differences in working memory capacity strongly suggests that the CDA

73 directly reflects the maintenance of visual information in working memory. The
74 contralateral nature and posterior scalp topography of the CDA is consistent with
75 neural generators in extrastriate visual areas (McCollough, Machizawa, Vogel 2007),
76 in line with the sensory recruitment model. The CDA is typically preceded by an N2pc
77 component that emerges around 200 ms post-stimulus, has a similar posterior scalp
78 topography (e.g. McCollough, Machizawa, Vogel 2007), and reflects the attentional
79 selection and encoding of task-relevant objects in ventral visual cortex (Eimer 1996;
80 Luck and Hillyard 1994).

81 While ERP markers of visual working memory are well established,
82 corresponding electrophysiological correlates of tactile working memory have not yet
83 been described. Here, we demonstrate the existence of two somatosensory ERP
84 components that are elicited during the encoding and maintenance of tactile stimuli in
85 working memory, and both show modality-specific topographies over primary
86 somatosensory cortex. We employed a task that was modelled on the delayed
87 match-to-sample task used in earlier studies of visual working memory (e.g., Vogel,
88 McCollough, Machizawa 2005; Vogel and Machizawa 2004). On each trial, a set of
89 tactile sample stimuli was followed after a 2000 ms retention period by tactile test
90 stimuli. Sample and test stimuli were delivered simultaneously to both hands, but the
91 memory task had to be performed for one of these hands only. Participants had to
92 encode and maintain tactile sample stimuli on the currently task-relevant hand, and to
93 match them to subsequent test stimuli on the same relevant hand. On low-load trials,
94 a single tactile stimulus had to be maintained and matched. On high-load trials, two
95 tactile pulses had to be memorized.

96 Results revealed the existence of two somatosensory ERP components that
97 have not yet been described in the literature on tactile attention and working memory.
98 During the retention interval, a sustained tactile contralateral delay activity (tCDA)

99 emerged with a modality-specific scalp distribution over somatosensory areas. This
100 tCDA component was sensitive to memory load and to individual differences in tactile
101 working memory capacity. It was preceded by a central contralateral negativity (N2cc
102 component) with a similar modality-specific topography that was also modulated by
103 working memory load. Analogous to the visual N2pc and CDA, these N2cc and tCDA
104 components reflect the spatially selective encoding and maintenance of task-relevant
105 information in tactile working memory.

106

107 **Materials and Methods**

108 **Participants**

109 Eighteen neurologically unimpaired paid adult participants were tested. The
110 study was conducted in accordance with the Declaration of Helsinki, and was
111 approved by the Psychology Ethics Committee, Birkbeck College. All participants
112 gave informed written consent prior to testing. Two participants were excluded from
113 analysis because their tactile WM capacity measured by Cowan's K (Cowan 2001)
114 was below 1. Sixteen participants remained in the sample (mean age 32 years, range
115 25-44 years, 3 male, 13 right-handed).

116

117 **Stimuli and task design**

118 Participants were seated in a dimly lit recording chamber, viewing a monitor
119 showing a central white fixation cross against a black background. Both hands were
120 covered from sight and were placed on a table at a distance of approximately 40 cm.
121 Eight mechanical tactile stimulators were attached to the distal phalanges of the
122 index, middle, ring and small fingers of the left and right hand. Stimulators were
123 driven by an eight-channel sound card (M-Audio, Delta 1010LT) and custom-built
124 amplifiers, controlled by Matlab (MathWorks, Natick, MA). Continuous white noise

125 was delivered via headphones to mask sounds produced by the tactile stimulators.
126 All tactile stimuli were 100 Hz sinusoids (duration: 200 ms; intensity: 0.37 N).

127 Figure 1 illustrates the experimental procedure. Each trial started with a set of
128 tactile sample stimuli that were delivered simultaneously to the left and right hand.
129 After a 2000 ms retention period, a set of tactile test stimuli was presented
130 simultaneously to both hands. Prior to the start of each block, instructions displayed
131 on the monitor informed participants whether the left or right hand was relevant in the
132 upcoming block. Participants had to decide whether sample and test stimulus
133 locations on this hand were identical (match trials) or different (mismatch trials). The
134 task-relevant hand was swapped after each experimental block. Two load conditions
135 were randomized within each block. In the *low-load condition*, one sample pulse was
136 presented with equal probability to one of the four fingers of the left hand and the
137 right hand. On match trials, the test pulse was delivered to the same finger of the
138 relevant hand as the sample pulse. On mismatch trials, one of the three other fingers
139 on that hand was stimulated at test. In the *high-load condition*, two sample pulses
140 were presented to two randomly selected fingers of the left hand and the right hand,
141 respectively. On match trials, test pulses were delivered to the same two fingers of
142 the relevant hand. On mismatch trials, at least one of the two test pulses was
143 presented to a different finger of that hand. Because one of the two sample locations
144 could be repeated at test on mismatch trials, participants had to retain the location of
145 both sample stimuli on the relevant hand to perform the task in the high-load
146 condition. Match and mismatch trials were equiprobable. On the currently task-
147 irrelevant hand, sample and test stimuli were also presented at matching or
148 mismatching locations, and this was independent of whether there was a match or
149 mismatch on the relevant hand.

150 Participants signalled a match or mismatch between sample and test on the
151 relevant hand with a vocal response (“a” for match and “e” for mismatch) that was
152 recorded with a headset microphone between 200 ms and 1700 ms after test
153 stimulus offset. A question mark replaced the fixation cross on the monitor during this
154 period. The interval between the offset of this question mark and the onset of the
155 sample pulses on the next trial varied between 800 and 1100 ms. The experiment
156 included ten blocks of 48 trials, with twelve trials per block for each of the four
157 combinations of high versus low load trials and match versus mismatch trials.
158 Instructions emphasized accuracy over speed, and the need to avoid head and arm
159 movements and to maintain central gaze fixation. Feedback on hit and correct
160 rejection rates was provided after each block. Two training blocks were run prior to
161 the first experimental block.

162

163 -----

164 Insert Figure 1 about here

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166

167 **Processing of EEG data**

168 EEG data, sampled at 500 Hz using a BrainVision amplifier, were DC-recorded
169 from 64 Ag/AgCl active electrodes at standard locations of the extended 10-20
170 system. Two electrodes at the outer canthi of the eyes monitored lateral eye
171 movements (horizontal electrooculogram, HEOG) and electrodes sites TP9/10 were
172 used as mastoid references. Continuous EEG data was referenced to the left mastoid
173 during recording, and was offline re-referenced to the arithmetic mean of both
174 mastoids and submitted to a 40Hz low-pass finite impulse response filter (Blackman

175 window, filter order 666). EEG epochs for the 2000 ms interval following sample
176 stimulus onset were computed relative to a 200 ms pre-stimulus baseline. Blind
177 source separation of EEG data was performed with the Independent Component
178 Analysis (ICA) algorithm implemented in the EEGLab toolbox (Delorme and Makeig
179 2004; Delorme, Sejnowski, Makeig 2007). Independent components related to
180 artifacts at anterior scalp regions (in particular, eye movements and blinks), were
181 identified by visual inspection and subtracted from the EEG data. To obtain reliable
182 ICA decompositions, a copy of the data was segmented into eight 250 ms frames
183 covering the 2000 ms retention period. These frames were corrected using whole-
184 epoch baselines to achieve data stationarity (cf., Groppe, Makeig, Kutas 2009)
185 without high-pass filtering, which would have removed slow brain potentials. The
186 copy was discarded after ICA decompositions had been applied to the original data
187 set. Epochs with lateral eye movements that escaped ICA artifact correction were
188 identified and removed with a differential step function on the bipolarized HEOG (step
189 width 100 ms, threshold 24 μ V). The resulting HEOG waveforms contained no
190 systematic eye gaze deflections towards the task-relevant hand (Figure 2, bottom
191 panel). After artifact rejection and elimination of trials with incorrect responses, 90.2%
192 of all epochs were retained for statistical analyses (low load: 93.4%; high load:
193 87.1%).

194

195 **Results**

196 **Behavioral performance**

197 Participants responded correctly on 97.1% of all low-load trials and 90.4% of
198 all high-load trials. Sensitivity indices (d') were analysed in a two-way repeated
199 measures ANOVA with the factors memory load (low, high) and relevant hand (left,
200 right). Performance was reduced with high load relative to low load ($F(1,15) = 71.728$,

201 $p < 10^{-6}$), and did not differ between blocks where the left or right hand was relevant
202 ($F(1,15) = 1.081, p > 0.3$). A significant memory load x relevant hand interaction
203 ($F(1,15) = 6.222, p = 0.025$) was due to the fact that the performance decrement with
204 high as compared to low memory load was larger when the memory task was
205 performed with the left hand (8.5%) relative to blocks where the right hand was
206 relevant (4.9%).

207 Mean vocal reaction times (RTs) in trials with correct responses were faster in
208 the low-load relative to the high-load condition (799 ms versus 817 ms; main effect of
209 memory load: $F(1,15) = 8.801, p = 0.010$). RTs did not differ between blocks where
210 the left or right hand was task-relevant ($F(1, 15) = 1.846, p > 0.1$). The memory load x
211 relevant hand interaction was significant ($F(1,15) = 5.25, p = 0.037$), as the RT costs
212 for the low-load versus high-load condition were larger when the memory task was
213 performed with the right hand (26 ms) relative to blocks where the left hand was
214 relevant (10 ms). In other words, there was an asymmetric speed-accuracy tradeoff
215 between the two hands for task performance in the high-load versus low-load
216 condition.

217

218 **Electrophysiological data**

219 Figure 2 shows ERP waveforms averaged across lateral central electrodes (FC3/4,
220 FC5/6, C3/4, C5/6, CP3/4, CP5/6) contralateral and ipsilateral to the task-relevant
221 hand for the 2000 ms interval between the bilateral sample stimulus and the
222 subsequent test stimulus. Results are shown separately for the low-load and high-
223 load conditions. Following the early sensory-evoked ERP components to the sample
224 stimulus, ERP waveforms were characterized by a gradually developing sustained
225 negativity that reached its maximal amplitude immediately before the onset of the test

226 stimuli. This sustained negativity that was present at contralateral as well as
227 ipsilateral electrodes reflects the Contingent Negative Variation (CNV; see Birbaumer
228 et al. 1990) that is elicited in anticipation of expected task-relevant events such as the
229 test stimulus set used in this study. More importantly, sample stimuli triggered a
230 transient enhanced negativity contralateral to the task-relevant hand. This N2cc
231 component emerged around 180 ms after sample stimulus onset, and its amplitude
232 was larger in the high-load as compared to the low-load condition. The N2cc was
233 followed by a sustained contralateral negativity (tCDA) that remained present
234 throughout the retention period. This tCDA component was larger when two tactile
235 stimuli had to be memorized relative to the low load condition. The topographical
236 maps in Figure 2 illustrate the scalp distribution of N2cc and tCDA components in the
237 low-load and high-load conditions. Data shown in these maps were collapsed across
238 blocks where the left or right hand was task-relevant by flipping ERPs at contralateral
239 electrodes in blocks with a left-hand memory task over the midline. Both N2cc and
240 tCDA components were maximal over somatosensory areas in the postcentral gyrus
241 and adjacent parietal regions (see also Figure 4 below).

242

243 -----

244 Insert Figure 2 about here

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246

247 Difference waveforms were computed by subtracting ERPs ipsilateral to the
248 currently task-relevant hand from contralateral ERPs. Statistical tests were conducted
249 on mean amplitudes of these difference waves for a time window centered on the
250 N2cc component (180-260 ms post-stimulus), and a second window centered on the

251 tCDA (300-2000 ms). Difference values that statistically differ from zero mark the
252 presence of reliable lateralized components in the ERP waveforms. The N2cc was
253 present in both the low-load ($t(15) = -5.593, p < 10^{-4}$) and high-load condition ($t(15) =$
254 $-7.037, p < 10^{-5}$). N2cc amplitudes were significantly larger with high relative to low
255 memory load ($t(15) = 4.235, p < 10^{-3}$). The tCDA component was present with low
256 load ($t(15) = -2.951, p = 0.010$) as well as with high memory load ($t(15) = -6.126, p <$
257 10^{-4}). Similar to the N2cc, tCDA amplitudes were significantly larger in the high-load
258 relative to the low-load condition ($t(15) = 3.801, p = 0.002$).

259 An additional analysis of mean amplitudes in the tCDA time window obtained
260 for the unsubtracted ERP waveforms revealed a main effect of contralaterality
261 (electrodes contralateral versus ipsilateral to the task-relevant hand; $F(1,15) =$
262 $38.006, p < 10^{-4}$) that interacted with load ($F(1,15) = 14.448, p = 0.002$), due to the
263 fact that the tCDA was larger in the high-load condition. There was also a main effect
264 of load ($F(1,15) = 14.862, p = 0.002$), with larger CNV components with high memory
265 load. This load-dependent modulation of CNV amplitudes was reliable at contralateral
266 as well as ipsilateral electrodes $t(15) = -4.500$ and $-2.481, p < 0.001$ and 0.026 ,
267 respectively).

268 Tactile working memory capacity was calculated for each individual participant
269 on the basis of their performance in the high-load condition, using the formula $K =$
270 $(hits + correct\ rejections - 1) \times 2$, where 2 denotes memory set size in this condition
271 (Cowan 2001). As illustrated in Figure 3, individual memory capacity was reliably
272 correlated with the difference of tCDA amplitudes between the high-load and low-load
273 conditions ($r = -0.640, p = 0.008$). Participants with higher tactile working memory
274 capacity showed a more pronounced increase of the tCDA component on trials with
275 high versus low memory load than participants with lower capacity. No correlation

276 was found between individual K values and the difference of N2cc amplitudes
277 between high- and low-load conditions ($p > 0.7$).

278 To obtain additional evidence for a link between tCDA amplitudes and
279 behavioral performance at the level of individual trials in the high-load condition, we
280 computed tCDA components in the high-load condition separately for trials with vocal
281 RTs above and below the median RT (with RT median splits conducted individually
282 for each participant and trial condition). Trials with fast responses were more
283 accurate than slow response trials (Cowan's K: fast = 1.786, slow = 1.453; $t(15) =$
284 6.362 , $p < 10^{-4}$). Critically, tCDA amplitudes were larger for fast as compared to slow
285 response trials ($-0.749 \mu\text{V}$ versus $-0.594 \mu\text{V}$), and this amplitude difference was
286 significant ($t(15) = -2.564$, $p = 0.022$).

287

288 -----

289 Insert Figure 3 about here

290 -----

291

292 An additional current source density (CSD) analysis was conducted to further
293 illustrate the modality-specific scalp topographies of the N2cc and tCDA components,
294 and to demonstrate that the selection of lateral central electrodes for the analysis of
295 these components was appropriate. ERP data were collapsed across the low- and
296 high-load conditions, after conversion of scalp potentials to surface Laplacians
297 ($\lambda = 10^{-5}$, iterations = 50, $m = 4$; cf. Tenke and Kayser 2012). This
298 transformation minimizes effects of volume conduction from remote sources, and
299 leads to a reference-independent representation of EEG/ERP data. CSD
300 topographies provide a conservative estimate of the neural generator patterns that

301 contribute to scalp-recorded ERPs (Nunez and Westdorp 1994; Tenke and Kayser
302 2012). Robust lateralized effects were found over somatosensory brain regions
303 (Figure 4), as demonstrated by significant differences of contra- minus ipsilateral
304 activity recorded at central electrodes in the time window of N2cc ($t(15) = -6.476$, $p <$
305 10^{-4}) and tCDA ($t(15) = -4.066$, $p = 0.001$). Apart from an almost significant
306 contralateral positivity at anterior regions during the N2cc time window ($t(15) = 2.107$,
307 $p = 0.052$), no statistically reliable lateralization was evident over posterior
308 (electrodes P3/4, P5/6, PO3/4, PO7/8) and anterior (electrodes AF3/4, AF7/8, F3/4,
309 F5/6) scalp regions (all p s > 0.2 ; see Figure 4).

310

311 -----

312 Insert Figure 4 about here

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315

316 Discussion

317 We employed a tactile memory task that was modelled on the delayed match-
318 to-sample task used in previous research on visual working memory (e.g., Vogel and
319 Machizawa 2004) to identify ERP correlates of the selection and maintenance of
320 task-relevant tactile stimuli. When participants memorized the spatial locations of one
321 or two tactile sample pulses on the left or the right hand, an enhanced negativity with
322 a centroparietal focus emerged contralateral to the hand where the memorized tactile
323 sample was delivered. This tCDA component was sensitive to tactile working memory
324 load, as it was larger on trials where participants had to remember two tactile
325 stimulus locations than when only a single tactile location had to be memorized

326 (Figure 2). The load-dependent increase of tCDA amplitudes was more pronounced
327 for participants with higher tactile working memory capacity than for individuals
328 whose capacity (measured by Cowan's K) was closer to 1 (Figure 3), mirroring
329 previous findings for the visual CDA component (Vogel and Machizawa 2004).
330 Furthermore, the tCDA component was reliably larger on trials with fast vocal
331 responses in the high-load condition, which were also more accurate than slow
332 responses. This demonstrates that the tCDA component is linked to behavioral
333 performance on individual trials. These observations strongly suggest that the tCDA
334 is an electrophysiological correlate of the maintenance of somatosensory information
335 in tactile working memory.

336 Analogous to the visual CDA, which has a modality-specific topography over
337 posterior visual cortex (McCollough, Machizawa, Vogel 2007), the tactile CDA
338 component emerged at contralateral central electrodes. The scalp topography of the
339 tCDA in a CSD-transformed map (Figure 4) also suggests neural generators that are
340 located within the somatosensory system. We conclude that the tCDA component
341 reflects the spatially selective activation of modality-specific brain regions
342 contralateral to the task-relevant hand during the retention of tactile stimuli in working
343 memory. These results provide new support for the sensory recruitment model, which
344 assumes that brain regions involved in the perceptual processing of sensory stimuli
345 are also active during the maintenance of these stimuli in working memory. It should
346 be noted that topographical distributions of CSD-transformed scalp maps only allow
347 relatively coarse approximations of the neural origins of components such as the
348 tCDA, and that the exact anatomical basis of this component needs to be determined
349 in future work.

350 Previous research has used transcranial magnetic stimulation (TMS; Harris et
351 al. 2002) and EEG source reconstruction techniques in studies with human

352 participants (Spitzer and Blankenburg 2011), as well as single-cell recordings in
353 monkeys (Romo and Salinas 2003) to show that the activity of neurons in primary
354 (SI) and secondary (SII) somatosensory cortex is modulated in tactile working
355 memory tasks. For example, a suppression of alpha activity indicative of attentional
356 processing was found over contralateral SI during the retention period of a
357 vibrotactile frequency discrimination task (Spitzer and Blankenburg 2011).
358 Asymmetric alpha band oscillations have also been suggested as the physiological
359 basis of the visual CDA component (van Dijk et al. 2010). Indirect evidence for a
360 recruitment of somatosensory brain areas comes from a tactile EEG study that used
361 task-irrelevant probe stimuli presented during the retention period to examine how
362 working memory influences somatosensory encoding (Katus, Andersen, Müller
363 2012). The retention of locations in working memory was mirrored by spatially
364 selective modulation of early ERP components to tactile probe stimuli with putative
365 origins in somatosensory areas such as SII (Frot and Mauguière 1999). These lines
366 of evidence point towards close links between the maintenance of tactile information
367 in working memory and the spatially specific activation of early somatosensory areas.
368 The critical new finding of the present study is the discovery of the tCDA component
369 that reflects the maintenance of tactile information in a sustained and load-dependent
370 manner. Because the tCDA is computed by comparing ERPs at electrodes
371 contralateral and ipsilateral to the location of memorized tactile events, it only reflects
372 the difference in the absolute activation of contralateral versus ipsilateral
373 somatosensory areas, and should therefore not be interpreted as evidence that
374 tactile working memory storage is exclusively contralateral. In fact, there is
375 electrophysiological evidence that ipsilateral somatosensory cortex may also be
376 involved in the maintenance of tactile pattern information (Li Hegner et al. 2007).

377 The tCDA component was preceded by an earlier contralateral negativity,
378 (N2cc component) which emerged around 180 ms after sample stimulus onset.
379 Similar to the tCDA, the N2cc showed a centroparietal scalp topography (see Figures
380 2 and 4), and was larger in the high-load as compared to the low-load condition. This
381 new N2cc component is likely to represent the somatosensory equivalent of the well-
382 known visual N2pc component. The N2pc is triggered at contralateral posterior
383 electrodes at a similar post-stimulus latency during the attentional selection of targets
384 among distractors in visual displays (Eimer 1996; Luck and Hillyard 1994), and
385 precedes the CDA in visual working memory studies that employ a similar delayed
386 match-to-sample task as the one used in the present study (e.g., Anderson, Vogel,
387 Awh 2011; McCollough, Machizawa, Vogel 2007). The load-dependent increase of
388 the tactile N2cc component observed in the present study mirrors previous findings
389 for the visual N2pc, which increases in size with the number of attended objects in
390 visual displays (e.g., Drew and Vogel 2008; Mazza and Caramazza 2011).

391 The absence of N2cc components in previous ERP studies of tactile spatial
392 attention is due to the fact that instead of employing bilateral stimuli, tactile events
393 were delivered to a single location on the left or right hand. In these studies, modality-
394 specific components of the somatosensory event-related potential, such as the P100
395 or N140, were found to be larger for tactile stimuli at currently attended as compared
396 to unattended positions (e.g., Forster and Eimer 2005), demonstrating that spatial
397 attention enhances the sensory processing of tactile events. Analogous to the visual
398 N2pc, which is elicited when target and distractor objects appear in both visual
399 hemifields, measurement of the N2cc component requires that relevant and irrelevant
400 tactile events are presented simultaneously to both hands, or to other homologous
401 locations on the left and right side of the body. Note that the modality-specific
402 somatosensory N2cc component found here is distinct from another ERP component

403 with the same label that has been observed in stimulus-response compatibility
404 experiments, and is linked to visuospatially guided response selection (Praamstra
405 and Oostenveld 2003). The question whether the effects of memory load on the N2cc
406 and tCDA components reflect load-sensitive modulations of two distinct processing
407 stages (i.e., the attentional selection and the subsequent storage of task-relevant
408 tactile information in working memory), or of a single memory maintenance stage that
409 temporally overlaps with the N2cc component needs to be investigated in future
410 studies where the demands on attentional target selection and working memory load
411 are independently manipulated. In addition to the N2cc and tCDA components, a
412 sustained bilateral CNV component that was observed in the interval between
413 sample and test stimuli was also modulated by memory load. This modulation may
414 primarily reflect differences in the preparation for the match/mismatch decision in
415 response to the test stimulus, which is more demanding in the high-load condition.
416 However, the presence of load effects at ipsilateral electrodes could in principle as
417 well reflect contributions of ipsilateral somatosensory cortex to working memory
418 maintenance (Li Hegner et al. 2007; see also van Ede, Lange, Maris 2013).

419 When considered together with the results of previous ERP investigations of
420 visual working memory (Anderson, Vogel, Awh 2011; McCollough, Machizawa, Vogel
421 2007; Vogel, McCollough, Machizawa 2005; Vogel and Machizawa 2004), the current
422 findings reveal striking similarities between the mechanisms that underlie the spatial
423 selection and selective maintenance of sensory stimuli in vision and touch. During
424 both visual and tactile working memory tasks, two contralateral ERP components are
425 elicited successively, with a highly similar time course in both modalities. N2pc and
426 N2cc components that emerge around 180 ms after sample display onset reflect
427 spatial selection during encoding of task-relevant visual or tactile information. The
428 subsequent CDA and tCDA components are linked to the sustained maintenance of

429 stored information during the retention period. The fact that the load-sensitive tCDA
430 component observed in this study showed a topography over lateral central
431 somatosensory areas (see Figure 4), while the visual CDA component is elicited over
432 lateral posterior visual cortex (McCollough, Machizawa, Vogel 2007) strongly
433 suggests that the maintenance of visual or tactile information in working memory
434 involves the activation of distinct modality-specific regions, in line with the sensory
435 recruitment model of working memory (D'Esposito 2007; Pasternak and Greenlee
436 2005; Postle 2006; Sreenivasan, Curtis, D'Esposito 2014). In both vision and touch,
437 neural networks that mediate the perceptual processing of sensory signals contribute
438 to the storage and maintenance of information in working memory.

439

440 **Acknowledgments**

441 This work was funded by the Deutsche Forschungsgemeinschaft (DFG grant KA
442 3843/1-1). We thank Sue Nicholas for invaluable help in setting up the hardware
443 used for tactile stimulation.

444

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543 **Figure Legends**

544 **Figure 1.** Illustration of the experimental setup. Participants memorized a tactile
545 sample set at one task-relevant hand to compare it with a test set on the same hand
546 after a 2 second retention period. Memory load was varied between trials (low load:
547 one pulse, high load: two pulses per hand). The relevant hand (left, right) was varied
548 between blocks. The example shown here illustrates a high-load trial where the
549 locations of tactile sample and test stimuli (symbolized by white dots) are identical at
550 the left hand (match), but not at the right hand (mismatch).

551

552 **Figure 2.** Grand mean ERPs elicited in the 2000 ms interval following sample
553 stimulus onset in the low-load and high-load conditions. ERPs were averaged across

554 lateral central electrode clusters contralateral (blue lines) and ipsilateral (red lines) to
555 the hand where the memory task was performed. Difference maps show the
556 topographical distribution of lateralized effects in the N2cc (bottom) and tCDA (top)
557 time windows. These maps represent the amplitude difference of contralateral minus
558 ipsilateral recordings, collapsed across blocks where the memory task was
559 performed with the left or right hand. Enhanced contralateral negativities are shown
560 in blue. The two bottom panels show difference waveforms for the low-load and high-
561 load condition, obtained by subtracting electrodes ipsilateral to the task-relevant hand
562 from contralateral electrodes, and HEOG difference waveforms, calculated by
563 subtracting HEOG electrodes ipsilateral to the task-relevant hand from contralateral
564 electrodes after artifact rejection. In these HEOG difference waves, any eye
565 movements towards the task-relevant hand would be reflected by negative
566 (downward) HEOG deflections.

567

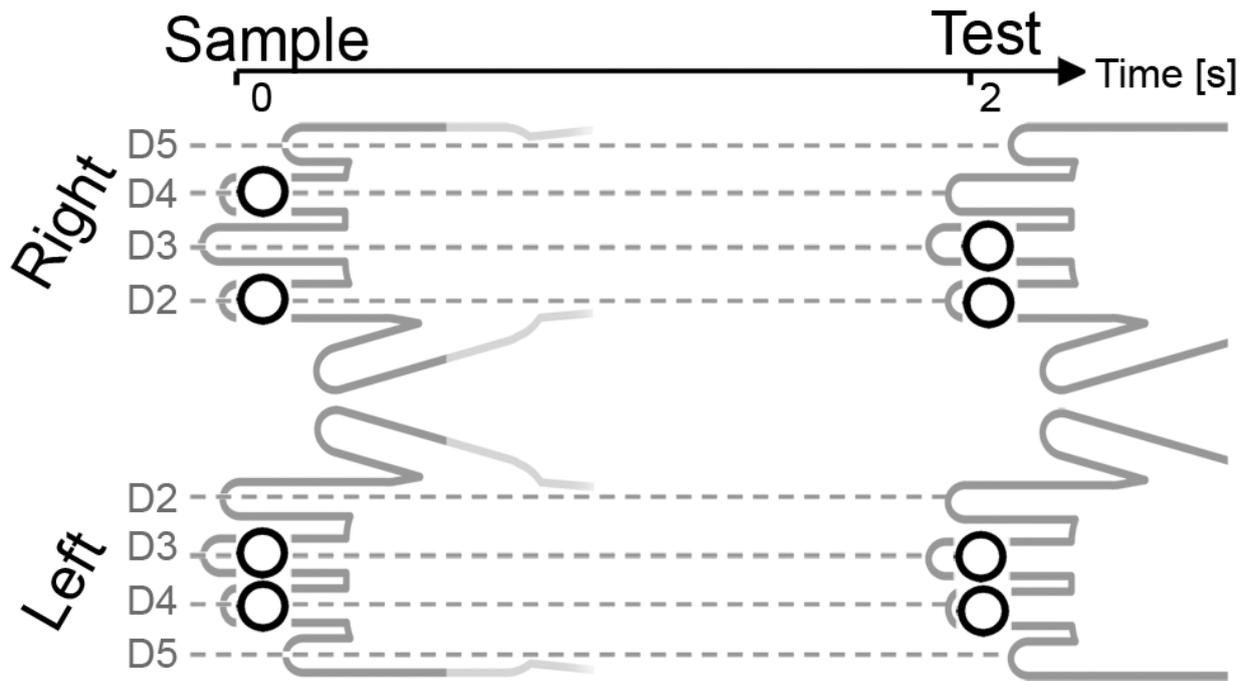
568 **Figure 3.** Correlation of individual participant's tactile working memory capacity K (x-
569 axis) and the increase of tCDA amplitudes in the high-load relative to the low-load
570 condition measured for each participant (y-axis). K was calculated on the basis of
571 individual performance in the high-load condition.

572

573 **Figure 4.** Grand mean current source density (CSD) topographical maps, showing
574 the scalp distribution of lateralized effects in the N2cc and tCDA time windows. These
575 maps represent the amplitude difference of contralateral minus ipsilateral recordings,
576 collapsed across blocks where the memory task was performed with the left or right
577 hand, and averaged across the low- and high-load conditions. Six electrodes at
578 lateral central scalp regions (black dots) were averaged for each recording cluster

579 (contra- and ipsilateral to the task-relevant hand). The presence of lateralized effects
580 was also tested for different sets of electrodes over anterior (white triangles) and
581 posterior (white crosses) scalp areas. Reliable lateralized effects were present only
582 for the central electrode cluster.

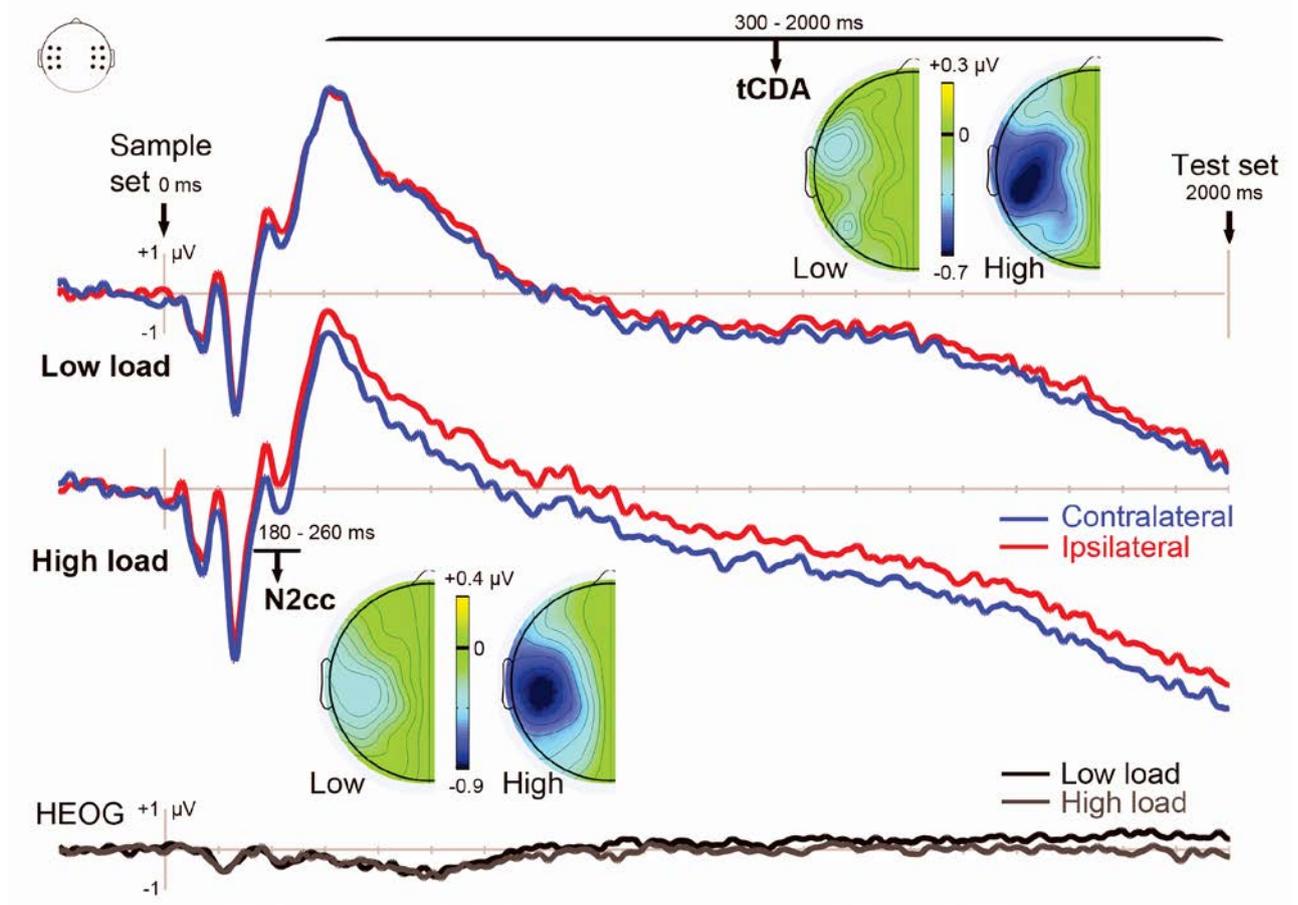
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585 FIGURE 1

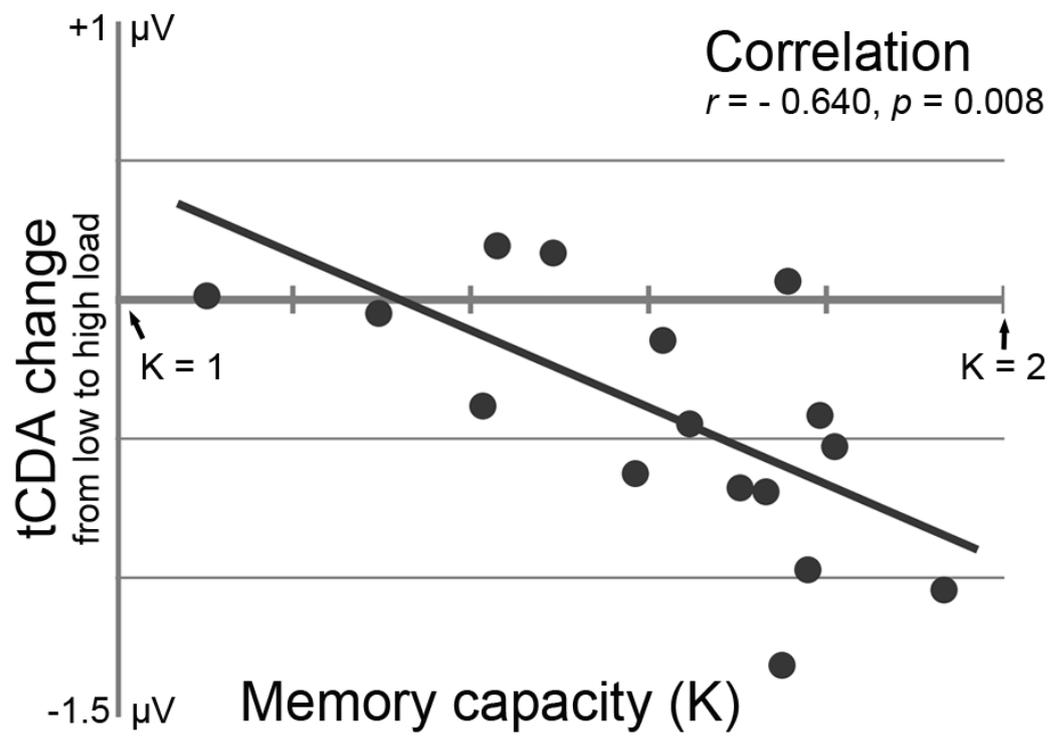
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588 FIGURE 2

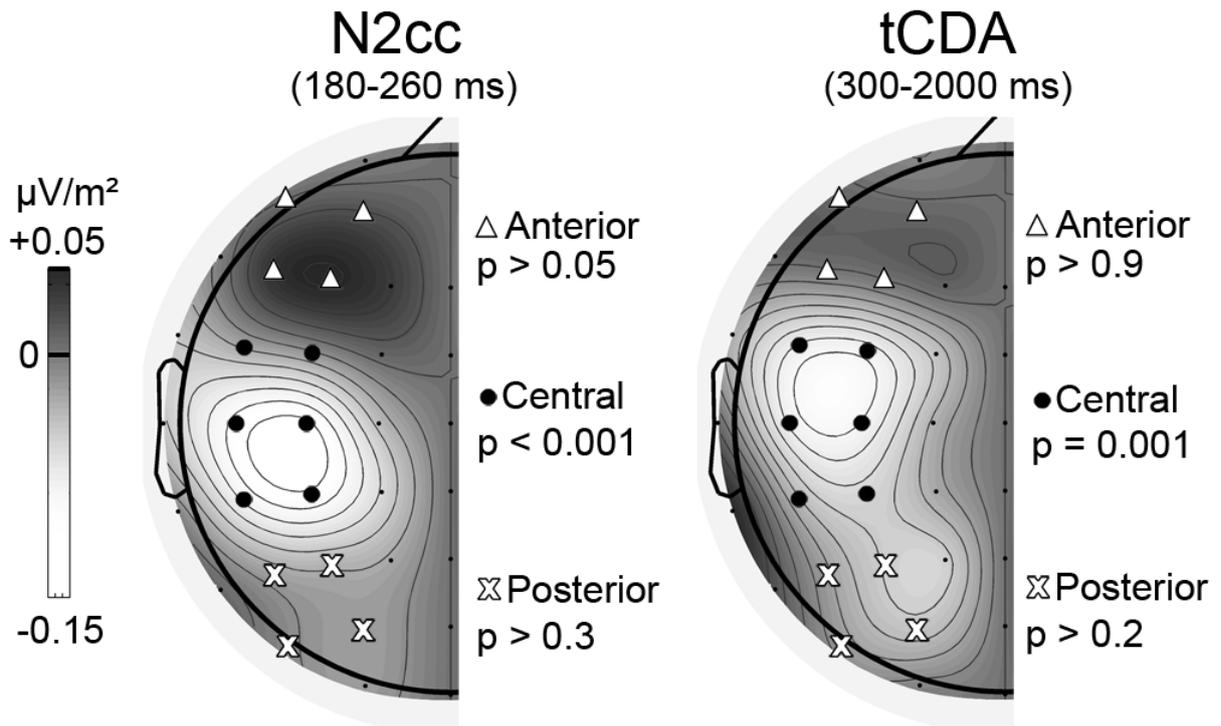
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591 FIGURE 3

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594 FIGURE 4