

Electrophysiological evidence for a sensory recruitment model of somatosensory working memory

Journal:	Cerebral Cortex
Manuscript ID:	CerCor-2014-00343.R2
Manuscript Type:	Original Articles
Date Submitted by the Author:	n/a
Complete List of Authors:	Katus, Tobias; Birkbeck College, Psychology Grubert, Anna; Birkbeck College, Psychology Eimer, Martin; Birkbeck College, Psychology
Keywords:	Electroencephalography (EEG), Selective Attention, Somatosensation, Working memory (WM), Event-related potentials (ERPs)



1	Full Manuscript Title
2	Electrophysiological evidence for a sensory recruitment model
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	^a Department 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: <u>t.katus@bbk.ac.uk</u>
16	
17	
18	
19	Conflict of Interest: The authors declare no competing financial interests.
20	
21	

of

23 Abstract

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

43 Introduction

Working memory (WM) is responsible for the active maintenance of information that is no longer perceptually present. Visual and tactile working memory are both assumed to be based on distributed neural networks that include prefrontal Page 3 of 28

Cerebral Cortex

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

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

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

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

Cerebral Cortex

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

107 Materials and Methods

108 Participants

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

117 Stimuli and task design

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

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

Page 7 of 28

Cerebral Cortex

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

163 -----

164 Insert Figure 1 about here

167 Processing of EEG data

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

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

 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,

Cerebral Cortex

 $p < 10^{-6}$), 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%).

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

218 Electrophysiological data

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

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

- 243 -----
- 244 Insert Figure 2 about here
- 245 -----

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

Page 11 of 28

Cerebral Cortex

tCDA (300-2000 ms). Difference values that statistically differ from zero mark the presence of reliable lateralized components in the ERP waveforms. The N2cc was present in both the low-load (t(15) = -5.593, $p < 10^{-4}$) and high-load condition (t(15) = -5.593) -7.037, $p < 10^{-5}$). N2cc amplitudes were significantly larger with high relative to low memory load (t(15) = 4.235, $p < 10^{-3}$). The tCDA component was present with low load (t(15) = -2.951, p = 0.010) as well as with high memory load (t(15) = -6.126, p < -6.12610⁻⁴). Similar to the N2cc, tCDA amplitudes were significantly larger in the high-load relative to the low-load condition (t(15) = 3.801, p = 0.002). An additional analysis of mean amplitudes in the tCDA time window obtained for the unsubtracted ERP waveforms revealed a main effect of contralaterality (electrodes contralateral versus ipsilateral to the task-relevant hand; F(1,15) =38.006, $p < 10^{-4}$) that interacted with load (F(1,15) = 14.448, p = 0.002), due to the fact that the tCDA was larger in the high-load condition. There was also a main effect

of load (F(1,15) = 14.862, p=0.002), with larger CNV components with high memory load. This load-dependent modulation of CNV amplitudes was reliable at contralateral as well as ipsilateral electrodes t(15) = -4.500 and -2.481, p < 0.001 and 0.026, respectively).

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

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

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

 288 -----

289 Insert Figure 3 about here

- 290 -----

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

Cerebral Cortex

2	
3	301
4	001
5	
6	302
0	
1	303
8	000
9	
10	304
11	
12	305
12	505
13	
14	306
15	
16	307
17	307
18	
10	308
20	
20	200
21	309
22	
23	040
24	310
25	
26	
20	311
21	
28	
29	312
30	
31	
32	313
22	
33	
34	314
35	-
36	045
37	315
38	
30	316
39	010
40	
41	317
42	
43	318
44	510
45	
40	319
40	
47	220
48	320
49	
50	321
51	
52	000
52	322
53	
54	323
55	525
56	
57	324
58	
50	375
59	520
60	

301	contribute to scalp-recorded ERPs (Nunez and Westdorp 1994; Tenke and Kaysei
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 ps > 0.2; see Figure 4).

11

12 Insert Figure 4 about here

Discussion 16

Jure 4). 17 We employed a tactile memory task that was modelled on the delayed match-18 to-sample task used in previous research on visual working memory (e.g., Vogel and 19 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 load, as it was larger on trials where participants had to remember two tactile 324 325 stimulus locations than when only a single tactile location had to be memorized

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

Analogous to the visual CDA, which has a modality-specific topography over posterior visual cortex (McCollough, Machizawa, Vogel 2007), the tactile CDA component emerged at contralateral central electrodes. The scalp topography of the tCDA in a CSD-transformed map (Figure 4) also suggests neural generators that are located within the somatosensory system. We conclude that the tCDA component reflects the spatially selective activation of modality-specific brain regions contralateral to the task-relevant hand during the retention of tactile stimuli in working memory. These results provide new support for the sensory recruitment model, which assumes that brain regions involved in the perceptual processing of sensory stimuli are also active during the maintenance of these stimuli in working memory. It should be noted that topographical distributions of CSD-transformed scalp maps only allow relatively coarse approximations of the neural origins of components such as the tCDA, and that the exact anatomical basis of this component needs to be determined 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 Page 15 of 28

Cerebral Cortex

1	
2	
3	
4	
5	
6	
7	
8	
9	
10	
11	
12	
13	
14	
10	
17	
18	
19	
20	
21	
22	
23	
24	
25	
26	
27	
28	
29	
30	
31	
32	
33	
34 25	
30	
37	
38	
39	
40	
41	
42	
43	
44	
45	
46	
47	
48	
49	
5U 54	
51	
52 52	
54	
55	
56	
57	
58	
59	
60	

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).

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

The absence of N2cc components in previous ERP studies of tactile spatial attention is due to the fact that instead of employing bilateral stimuli, tactile events were delivered to a single location on the left or right hand. In these studies, modality-specific components of the somatosensory event-related potential, such as the P100 or N140, were found to be larger for tactile stimuli at currently attended as compared to unattended positions (e.g., Forster and Eimer 2005), demonstrating that spatial attention enhances the sensory processing of tactile events. Analogous to the visual N2pc, which is elicited when target and distractor objects appear in both visual hemifields, measurement of the N2cc component requires that relevant and irrelevant tactile events are presented simultaneously to both hands, or to other homologous locations on the left and right side of the body. Note that the modality-specific somatosensory N2cc component found here is distinct from another ERP component Page 17 of 28

Cerebral Cortex

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

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

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

440 Acknowledgments

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

References

446 Anderson DE, Vogel EK, Awh E. 2011. Precision in visual working memory reaches a

447 stable plateau when individual item limits are exceeded. J Neurosci. 31(3):1128–

448 1138.

449 Birbaumer N, Elbert T, Canavan AG, Rockstroh, B 1990. Slow potentials of the

450 cerebral cortex and behavior. Physiol Rev. 70(1): 1-41.

451 Cowan N. 2001. The magical number 4 in short-term memory: a reconsideration of

452 mental storage capacity. Behav Brain Sci. 24(1):87-114x.

Page 19 of 28

Cerebral Cortex

1	9

2		
2 3 4	453	Curtis CE, D'Esposito M. 2003. Persistent activity in the prefrontal cortex during
- 5 6	454	working memory. Trends Cogn Sci. 7(9):415–423.
7 8	455	Curtis CE, Rao VY, D'Esposito M. 2004. Maintenance of spatial and motor codes
9 10	456	during oculomotor delayed response tasks. J Neurosci. 24(16):3944–3952.
11 12	457	Delorme A, Makeig S. 2004. EEGLAB: an open source toolbox for analysis of single-
13 14 15	458	trial EEG dynamics including independent component analysis. J Neurosci
15 16 17	459	Methods. 134(1):9–21.
18 19	460	Delorme A, Sejnowski T, Makeig S. 2007. Enhanced detection of artifacts in EEG
20 21	461	data using higher-order statistics and independent component analysis.
22 23	462	Neuroimage. 34(4):1443–1449.
24 25 26	463	D'Esposito M. 2007. From cognitive to neural models of working memory. Philos
20 27 28	464	Trans R Soc Lond B Biol Sci. 362(1481):761–772.
29 30	465	Drew T, Vogel EK. 2008. Neural measures of individual differences in selecting and
31 32	466	tracking multiple moving objects. J Neurosci. 28(16):4183–4191.
33 34	467	Eimer M. 1996. The N2pc component as an indicator of attentional selectivity.
35 36 37	468	Electroencephalogr Clin Neurophysiol. 99(3):225–234.
38 39	469	Forster B, Eimer M. 2005. Covert attention in touch: Behavioral and ERP evidence
40 41	470	for costs and benefits. Psychophysiology. 42(2):171–179.
42 43	471	Frot M, Mauguière F. 1999. Timing and spatial distribution of somatosensory
44 45 46	472	responses recorded in the upper bank of the sylvian fissure (SII area) in humans.
40 47 48	473	Cereb Cortex. 9(8):854–863.
49 50	474	Fuster JM, Alexander GE. 1971. Neuron activity related to short-term memory.
51 52	475	Science. 173(3997):652–654.
53 54	476	Groppe DM, Makeig S, Kutas M. 2009. Identifying reliable independent components
55 56	477	via split-half comparisons. Neuroimage. 45(4):1199–1211.
57 58 59		

478	Harris JA, Miniussi C, Harris IM, Diamond ME. 2002. Transient storage of a tactile
479	memory trace in primary somatosensory cortex. J Neurosci. 22(19):8720-8725.
480	Harrison SA, Tong F. 2009. Decoding reveals the contents of visual working memory
481	in early visual areas. Nature. 458(7238):632–635.
482	Kaas AL, van Mier H, Visser M, Goebel R. 2013. The neural substrate for working
483	memory of tactile surface texture. Hum Brain Mapp. 34(5):1148–1162.
484	Katus T, Andersen SK, Müller MM. 2012. Maintenance of tactile short-term memory
485	for locations is mediated by spatial attention. Biol Psychol. 89(1):39–46.
486	Kostopoulos P, Albanese M, Petrides M. 2007. Ventrolateral prefrontal cortex and
487	tactile memory disambiguation in the human brain. Proc Natl Acad Sci USA.
488	104(24):10223–10228.
489	Lee SH, Kravitz DJ, Baker CI. 2013. Goal-dependent dissociation of visual and
490	prefrontal cortices during working memory. Nature Neurosci. 16(8), 997-999.
491	Li Hegner Y, Lutzenberger W, Leiberg S, Braun C. 2007. The involvement of
492	ipsilateral temporoparietal cortex in tactile pattern working memory as reflected in
493	beta event-related desynchronization. Neuroimage. 37(4): 1362–1370.
494	Lewis-Peacock JA, Drysdale AT, Oberauer K, Postle BR. 2012. Neural evidence for a
495	distinction between short-term memory and the focus of attention. J Cogn
496	Neurosci. 24(1): 61–79.
497	Luck SJ, Hillyard SA. 1994. Spatial filtering during visual search: Evidence from
498	human electrophysiology. J Exp Psychol Hum Percept Perform. 20(5):1000–1014.
499	Mazza V, Caramazza A. 2011. Temporal brain dynamics of multiple object
500	processing: the flexibility of individuation. PLoS ONE. 6(2):e17453.
501	McCollough AW, Machizawa MG, Vogel EK. 2007. Electrophysiological measures of
502	maintaining representations in visual working memory. Cortex. 43(1):77–94.

Page 21 of 28

Cerebral Cortex

\mathbf{a}	4
/	1
_	

1 2		
2 3 4	503	Nunez PL, Westdorp AF. 1994. The surface Laplacian, high resolution EEG and
5	504	controversies. Brain Topogr. 6(3):221–226.
7 8	505	Pasternak T, Greenlee MW. 2005. Working memory in primate sensory systems. Nat
9 10	506	Rev Neurosci. 6(2):97–107.
11 12	507	Postle BR. 2005. Delay-period activity in the prefrontal cortex: one function is sensory
13 14 15	508	gating. J Cogn Neurosci. 17(11):1679–1690.
16 17	509	Postle BR. 2006. Working memory as an emergent property of the mind and brain.
18 19	510	Neuroscience. 139(1):23–38.
20 21	511	Postle BR, Awh E, Serences JT, Sutterer DW, D'Esposito M. 2013. The positional-
22 23 24	512	specificity effect reveals a passive-trace contribution to visual short-term memory.
24 25 26	513	PLoS ONE. 8(12): e83483.
27 28	514	Praamstra P, Oostenveld R. 2003. Attention and movement-related motor cortex
29 30	515	activation: a high-density EEG study of spatial stimulus-response compatibility.
31 32	516	Brain Res Cogn Brain Res. 16(3):309–322.
33 34 35	517	Romo R, Salinas E. 2003. Flutter discrimination: neural codes, perception, memory
36 37	518	and decision making. Nat Rev Neurosci. 4(3):203–218.
38 39	519	Spitzer B, Blankenburg F. 2011. Stimulus-dependent EEG activity reflects internal
40 41	520	updating of tactile working memory in humans. Proc Natl Acad Sci USA.
42 43 44	521	108(20):8444–8449.
45 46	522	Sreenivasan KK, Curtis CE, D'Esposito M. 2014. Revisiting the role of persistent
47 48	523	neural activity during working memory. Trends Cogn Sci. 18(2), 82-89.
49 50	524	Supèr H, Spekreijse H, Lamme VA. 2001. A neural correlate of working memory in
51 52 53	525	the monkey primary visual cortex. Science. 293(5527):120–124.
55 55	526	Tenke CE, Kayser J. 2012. Generator localization by current source density (CSD):
56 57	527	implications of volume conduction and field closure at intracranial and scalp
58 59 60	528	resolutions. Clin Neurophysiol. 123(12):2328–2345.

529	van Dijk H, van der Werf J, Mazaheri A, Medendorp WP, Jensen O. 2010.
530	Modulations in oscillatory activity with amplitude asymmetry can produce
531	cognitively relevant event-related responses. Proc Natl Acad Sci USA. 107(2):
532	900–905.
533	van Ede F, de Lange FP, Maris E. 2013. Anticipation increases tactile stimulus
534	processing in the ipsilateral primary somatosensory cortex. Cereb Cortex.
535	Doi: 10.1093/cercor/bht111.
536	Vogel EK, McCollough AW, Machizawa MG. 2005. Neural measures reveal individual
537	differences in controlling access to working memory. Nature. 438(7067):500–503.
538	Zhou YD, Fuster JM. 1996. Mnemonic neuronal activity in somatosensory cortex.
539	Proc Natl Acad Sci USA. 93(19):10533–10537.
540	
541	
542	
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	

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

Cerebral Cortex

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

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

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

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



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

86x50mm (300 x 300 DPI)



Figure 2. Grand mean ERPs elicited in the 2000 ms interval following sample stimulus onset in the low-load and high-load conditions. ERPs were averaged across lateral central electrode clusters contralateral (blue lines) and ipsilateral (red lines) to the hand where the memory task was performed. Difference maps show the topographical distribution of lateralized effects in the N2cc (bottom) and tCDA (top) time windows.
 These maps represent the amplitude difference of contralateral minus ipsilateral recordings, collapsed across blocks where the memory task was performed with the left or right hand. Enhanced contralateral negativities are shown in blue. The two bottom panels show difference waveforms for the low-load and high-load condition, obtained by subtracting electrodes ipsilateral to the task-relevant hand from contralateral electrodes after artifact rejection. In these HEOG difference waves, any eye movements towards the task-relevant hand would be reflected by negative (downward) HEOG deflections.

180x148mm (300 x 300 DPI)





Figure 3. Correlation of individual participant's tactile working memory capacity K (x-axis) and the increase of tCDA amplitudes in the high-load relative to the low-load condition measured for each participant (yaxis). K was calculated on the basis of individual performance in the high-load condition. 86x61mm (300 x 300 DPI)





Figure 4. Grand mean current source density (CSD) topographical maps, showing the scalp distribution of lateralized effects in the N2cc and tCDA time windows. These maps represent the amplitude difference of contralateral minus ipsilateral recordings, collapsed across blocks where the memory task was performed with the left or right hand, and averaged across the low- and high-load conditions. Six electrodes at lateral central scalp regions (black dots) were averaged for each recording cluster (contra- and ipsilateral to the task-relevant hand). The presence of lateralized effects was also tested for different sets of electrodes over anterior (white triangles) and posterior (white crosses) scalp areas. Reliable lateralized effects were present only for the central electrode cluster.

86x52mm (300 x 300 DPI)