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Shifts of spatial attention in visual and tactile working memory are

controlled by independent modality-specific mechanisms

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Abstract

The question whether the attentional control of working memory (WM) is shared across sensory modalities remains controversial. Here, we investigated whether attention shifts in visual and tactile WM are regulated independently. Participants memorized visual and tactile targets in a first memory sample set (S1) before encoding targets in a second sample set (S2). Importantly, visual or tactile S2 targets could appear on the same side as the corresponding S1 targets, or on opposite sides, thus requiring shifts of spatial attention in visual or tactile WM. The activation of WM representations in modality-specific visual and somatosensory areas was tracked by recording visual and tactile contralateral delay activity (CDA/tCDA). CDA/tCDA components emerged contralateral to the side of visual or tactile S1 targets, and reversed polarity when S2 targets in the same modality appeared on the opposite side. Critically, the visual CDA was unaffected by the presence versus absence of concurrent attention shifts in tactile WM, and the tactile CDA remained insensitive to visual attention shifts. Visual and tactile WM performance was also not modulated by attention shifts in the other modality. These results show that the dynamic control of visual and tactile WM activation processes operates in an independent modality-specific fashion.

Introduction

Working memory (WM) refers to the set of cognitive and neural mechanisms that are responsible for the maintenance of perceptual information that is no longer physically present, and for making this information accessible to other psychological

47 processes. Several lines of evidence point towards a critical role of spatial attention

48 during the encoding and storage of sensory signals in WM (Awh, Vogel, Oh 2006).

49 WM maintenance relies on frontoparietal networks that are also involved in the control

50 of spatial attention (Awh and Jonides 2001). The sustained activity of neurons in

51 prefrontal cortex that is observed during the delay period of WM tasks is selectively

52 tuned to memorized object locations on the contralateral side (Funahashi 2013). The

53 role of spatial attention for feature binding and the formation of object-based

54 representations in WM has been demonstrated by space-based competition effects

55 (Robertson 2003). For example, decreasing the spatial distance between competing

56 stimuli reduces WM precision and increases binding errors in WM (Emrich and Ferber

57 2012; Ahmad et al. 2017).

58 Electrophysiological studies of WM have provided additional evidence for links

59 between WM maintenance and space-based attentional control processes. Spatial

60 location appears to be represented in an obligatory fashion in visual WM, even when

61 it is task-irrelevant (Foster et al. 2017; Kuo et al. 2009; Katus, Andersen, Müller 2012).

62 The maintenance of sensory signals in WM during the delay periods of lateralized

63 visual and tactile change detection tasks is associated with spatially selective

64 modulations of event-related potentials (ERPs). Visual WM maintenance gives rise to

65 a sustained negativity contralateral to the to-be-memorized visual objects (Vogel and

66 Machizawa 2004), and an analogous contralateral negativity has also been found in

67 tactile WM tasks (Katus, Grubert, Eimer 2015). This visual contralateral delay activity

68 (CDA) and its tactile equivalent (tCDA component) have modality-specific

69 topographies over visual and somatosensory cortex, respectively. They reflect

70 spatially selective modulations of neural activity in modality-specific sensory-

71 perceptual cortical areas, in line with the sensory recruitment account of WM (Postle

72 2006). The fact that CDA and tCDA amplitudes both increase with the number of visual

73 or tactile stimuli that have to be maintained, and the fact that both are sensitive to

74 individual differences in WM capacity (Vogel and Machizawa 2004; Katus, Grubert,

75 Eimer 2015) demonstrate that these two components are linked to WM maintenance

76 processes in vision and touch.

77   Evidence that CDA components do not reflect the generic storage of content in

78 WM, but more specifically the attentional activation of WM representations comes from

79 studies that used retro-cue and sequential loading procedures (see also McElree,

80 2001; Oberauer and Hein, 2012, for discussions of links between attention and WM

81 storage). In retro-cue experiments, observers initially encode stimuli on both sides,

82 before a cue indicates the task-relevant items for the current trial. Retro-cues trigger

83 shifts of attention towards representations that are already stored in WM. These

84 attention shifts were found to modulate the CDA and tCDA components in visual

85 (Eimer and Kiss 2010) and tactile (Katus, Müller, Eimer 2015) retro-cue experiments.

86 In sequential loading tasks, participants memorize task-relevant target stimuli in two

87 sequentially presented sample sets (S1, S2). When the target items in S1 and S2 are

88 presented on opposite sides, CDA components are initially triggered contralateral to

89 the S1 targets, but then reverse polarity during the S2-period, reflecting the task-

90 relevant item locations in the second sample set. This polarity reversal was observed

91 for the tCDA in a tactile WM experiment (Katus and Eimer 2015) and for the CDA

92 during the sequential loading of visual WM (Berggren and Eimer 2016), indicating

93 shifts of spatial attention towards the contralateral side of somatotopic or retinotopic

94 space during the S2-period (see also Drew et al., 2014b, for an analogous polarity

95 reversal of visual CDA components during continuous object tracking when visual

96 objects cross the vertical midline). Importantly, even though visual and tactile CDA

components were elicited contralateral to S2 sample items on opposite-side trials in these studies, memory performance for S1 items was still well above chance, indicating that information about S1 was retained in WM, although presumably in a different attention-independent format (see also Lewis-Peacock et al. 2012; LaRocque et al. 2013; for additional fMRI and EEG evidence for activity-silent WM storage mechanisms).

If top-down spatial attention modulates the storage of sensory stimuli in WM, the important question arises how these attentional control processes operate in multisensory WM tasks where items from different modalities have to be encoded and maintained simultaneously. It has been argued that WM maintenance processes in such multisensory tasks rely on modality-unspecific central attentional resources (Cowan 2011). If this is correct, the ability to retain multiple stimuli from different modalities in WM should be strongly affected by the spatial correspondence of these stimuli. For example, visual and tactile sample stimuli should be maintained better when they are presented on the same side than when they appear on opposite sides. In the latter case, attention would have to be allocated to opposite sides in different modalities, which will be difficult if these attention shifts are mediated by a single modality-unspecific control system. Evidence for strong spatial synergies between attentional control processes in vision, audition, and touch have indeed been identified in previous behavioral and electrophysiological experiments on crossmodal links in spatial attention (Spence and Driver 1996; Eimer, van Velzen, Driver 2002), suggesting that attention shifts in different modalities are either closely linked or controlled by shared central mechanisms.

Previous studies of multimodal WM have found performance costs in bimodal WM tasks relative to unimodal baseline conditions (e.g., Cowan, Saults, Blume 2014;

122 Fougnie and Marois 2011; Saults and Cowan 2007), suggesting that some aspect of

123 WM processing in a given modality is impaired when items in another modality have

124 to be simultaneously maintained. If these bimodal costs were associated with the need

125 to coordinate shared spatially selective attentional control processes across sensory

126 modalities, they should be particularly pronounced under conditions where to-be-

127 memorized items in different modalities are presented at spatially incongruent

128 locations. Such spatial congruency effects on multimodal WM performance have not

129 yet been investigated systematically. One exception is a recent ERP study from our

130 lab (Katus and Eimer 2016) where participants memorized two tactile and two visual

131 sample stimuli that were either presented on the same side or on opposite sides. In

132 same-side blocks, visual and tactile CDA components were elicited over the same

133 hemisphere, each with their typical modality-specific topography. In opposite-side

134 blocks, these components emerged over different hemispheres, contralateral to the

135 respective task-relevant visual and tactile sample items. Critically, visual and tactile

136 CDAs were elicited at the same time and were identical in amplitude in same-side and

137 opposite-side blocks, and WM performance did not differ between these two types of

138 blocks. The absence of any behavioral or electrophysiological evidence for impaired

139 visual and tactile WM maintenance processes in the opposite-side blocks of this

140 experiment suggests that these processes are controlled by parallel and entirely

141 independent modality-specific mechanism of spatial attention.

142 The apparent independence of space-based attentional control processes

143 during visual and tactile WM maintenance suggested by the results of this previous

144 EEG experiment (Katus and Eimer 2016) contrasts with previous evidence for

145 crossmodal synergies in spatial attention (Eimer and van Velzen 2002; Spence and

146 Driver 1996; Eimer, van Velzen, Driver 2002), and is also inconsistent with claims that

147   WM storage in multisensory tasks is based on shared central control mechanisms

148   (Cowan 2011). It is possible that these results are specific to the particular task

149   conditions that were realized in this experiment. The fact that the side of task-relevant

150   visual and tactile sample items was specified in advance and remained constant for

151   an entire block enabled participants to activate constant attentional task sets for the

152   relevant visual and tactile locations prior to the start of each block. Furthermore,

153   because all sample stimuli were presented simultaneously, no dynamic re-allocations

154   of spatial attention between WM representations were required in this experiment.

155   These two factors may have been responsible for the absence of any evidence of

156   impaired WM maintenance in the opposite-side blocks of our previous CDA study

157   (Katus and Eimer 2016). Spatial synergies in the attentional control of WM

158   maintenance in bimodal tasks may emerge primarily under conditions where the

159   locations of task-relevant memory sample items vary unpredictably across trials, and

160   where attention has to shift rapidly between WM representations within and across

161   sensory modalities. This was tested in the present study.

162   We employed sequential loading procedures in bimodal visual/tactile WM

163   tasks. At the start of each trial, bimodal sample sets (S1) were presented, which were

164   followed after a delay period by a second sample set (S2), and then, after another

165   delay period, by a memory test display (vision or touch). The identity of the to-be-

166   memorized visual sample items was indicated by their shape (Experiment 1) or color

167   (Experiment 2), and task-relevant tactile items were defined by stimulus waveform

168   (pulsed versus continuous; in Experiments 1b and 2). These relevant visual and tactile

169   items (targets) were always accompanied by task-irrelevant items on the opposite side

170   of the sample sets. The critical manipulation concerned the need to shift attention in

171   either touch or vision in the period following S2. Tactile or visual S2 target items were

172 presented either on the same side or on the opposite side as the S1 targets in the

173 same modality. To track the activation of visual and tactile WM representations, we

174 measured CDA and tCDA components during the periods following S1 and S2.

175   In Experiment 1, the sequential loading task was performed for one primary

176 modality (vision in Experiment 1a, touch in Experiment 1b) and a secondary modality

177 (touch or vision in Experiments 1a and 1b, respectively). S1 always contained items

178 in both modalities, and task-relevant visual and tactile items were always presented

179 on the same side. S2 only contained primary-modality items, and the to-be-memorized

180 targets appeared unpredictably either on the same side as the target items in S1 or on

181 the opposite side (stay/shift trials; see Figure 1). Participants were instructed to

182 memorize the primary-modality target items in S1 and S2, while also maintaining the

183 secondary-modality S1 targets across both delay periods. Memory was unpredictably

184 tested for either modality. For vision, participants reported the presence/absence of a

185 color change between task-relevant visual sample and test stimuli. For touch, the

186 presence/absence of a location change had to be reported. In addition to these

187 bimodal task blocks, there were also unimodal baseline blocks where stimulus

188 presentation procedures were identical but WM was always tested for the primary

189 modality, so that S1 items for the secondary modality could be entirely ignored.

190   In unimodal blocks, reliable CDA components should only be elicited in the

191 currently task-relevant primary modality, but should not be present over sensory areas

192 for the secondary irrelevant modality. Visual and tactile CDA components for the

193 primary modality were expected to change polarity on switch trials but not on stay

194 trials, reflecting the dynamic re-allocation of spatial attention in response to S2 (Katus

195 and Eimer 2015; Berggren and Eimer 2016). If WM maintenance in vision and touch

196 relies on shared space-based attentional control mechanisms, spatial synergies

between visual and tactile WM should result in crossmodal interference effects from vision to touch, and vice versa, on shift trials. This spatial interference should result in general costs for WM performance on shift as compared to stay trials, and also affect visual and tactile CDA components. For the primary modality, the requirement to maintain a constant attentional focus in the other (secondary) modality should attenuate or eliminate the CDA polarity reversal in response to S2 on shift trials, relative to unimodal baseline blocks. For the secondary modality, the need to shift versus maintain the attentional focus in the other (primary) modality should affect visual or tactile CDA components in the interval following S2. The alternative possibility is that top-down spatial attention operates in a strictly independent modality-specific fashion within visual and tactile WM, even under conditions where attention has to be rapidly re-allocated between WM representations. In this case, there should be no spatial synergies between attentional control processes in vision and touch, no crossmodal interference effects on WM performance on bimodal shift trials, and critically, no differences between shift and stay trials for visual and tactile CDA components. Bayesian statistics (Rouder et al. 2017) were employed to confirm the reliability of any such null-effects.

In Experiment 2, S1 and S2 both contained target items from both modalities. As in Experiment 1, the task-relevant tactile and visual items in S1 always appeared on the same side. The location where visual and tactile target items in S2 were presented (same versus side as in S1) was varied randomly and orthogonally, resulting in four different trial conditions (both stay; both switch; vision stay/tactile switch; vision switch/tactile stay). In this experiment, memory was tested for locations in both vision and touch.

Materials and methods

Participants

All participants were neurologically unimpaired and gave informed written consent prior to testing. 49 paid volunteers participated in the three experiments. 5 participants were excluded from statistical analysis due to excessive EEG artifacts (1 participant each in Experiments 1a and 1b, 3 participants in Experiment 2), resulting in a final sample of 44 participants (Experiment 1a: 12 participants, 30y mean age, 7 female, 10 right-handed; Experiment 1b: 16 participants, 29y mean age, 11 female, 13 right-handed; Experiment 2: 16 participants, 30y mean age, 10 female, 14 right-handed). All experiments were conducted in accordance with the Declaration of Helsinki, and were approved by the Psychology Ethics Committee, Birkbeck, University of London.

Stimulus material and apparatus

Visual stimuli were shown for 200 ms against a dark background on a 22 inch monitor (Samsung wide SyncMaster 2233; 1280 x 1024 resolution, 100 Hz refresh rate, 16 ms response time) at a viewing distance of 100 cm. Tactile stimuli were presented for 200 ms by eight mechanical stimulators on the left and right hands' distal phalanges of the index, middle, ring and small fingers. The stimulators were driven by custom-built amplifiers, using an eight-channel sound card (M-Audio, Delta 1010LT) controlled by Matlab routines (MathWorks, Natick, MA). Continuous pink noise was played on headphones to mask any sounds produced by the tactile stimulators. A headset microphone recorded vocal responses in the 1800 ms response period after each trial ('a' for match, 'e' for mismatch; details below).

247

Task design

Experiment 1a. Vision and touch were primary and secondary modality, respectively. The first bimodal memory sample set (S1, load: 2 visual and 2 tactile targets) was followed by a second unimodal visual sample set (S2, load: 2 visual targets), and a unimodal memory test stimulus set (50% tactile or visual in bimodal blocks, 100% visual in unimodal blocks). The three sets were separated by intervals of 1000 ms. Each visual sample set included two squares on one monitor side and two circles on the other side (size: 0.63° of visual angle each). The side where a particular shape appeared was independently randomized for S1 and S2. On stay trials (50%), the shapes' locations did not change across S1 and S2. On shift trials (50%), shapes locations were swapped (i.e., squares were followed by circles on one monitor side, and circles were followed by squares on the other side); see Figure 1A. The shape that defined the task-relevant visual sample stimuli (targets: circle or square) was counterbalanced across participants, who memorized the targets' colors for both S1 and S2. For the four task-relevant target shapes in the S1 and S2 displays, four out of six possible colors were selected on each trial (CIE color coordinates: red = .627/.336; green = .263/.568; blue = .189/.193; yellow = .422/.468; cyan = .212/.350; magenta = .289/.168). The four colors of the four task-irrelevant shapes in these displays were selected independently from this set of six colors. Visual sample item pairs were shown bilaterally in invisible 2-by-2 matrices (vertical eccentricity relative to stimulus center: 0.46° of visual angle; horizontal eccentricity: 1.60° inner quadrants, 2.58° outer quadrants). The sample pair on the left appeared in the top left and bottom right locations, and the pair on the right in the top right and bottom left locations, or vice versa. The task-relevant samples in S1 and S2 were always presented at different

272   locations, so that four colors at four different locations had to be memorized after S2;

273   see Figure 1. Visual test sets involved four target shapes in a 2-by-2 matrix at central

274   fixation (0.46° horizontal and vertical eccentricity). On visual match trials (50%), the

275   four memorized target colors were repeated. Their spatial arrangement (top/bottom,

276   left/right) matched the location of the memorized colors in the S1 and S2 displays. On

277   visual mismatch trials (50%), the color one of the four test display items was replaced

278   by a different not-memorized color.

279   Four identical tactile sample stimuli (100 Hz vibrations, intensity: 0.37 N) were

280   presented to two randomly selected fingers on the left and right hand, simultaneously

281   with the visual S1 displays. In bimodal blocks, participants were instructed to

282   memorize the locations of the tactile samples on the same side where the task-

283   relevant visual S1 sample shapes were presented. On half of all trials, pairs of tactile

284   stimuli were presented to the left and right hand at memory test. On tactile match trials

285   (50%), the two tactile test items on the task-relevant hand appeared at the same

286   locations as in S1. On tactile mismatch trials (50%), one of these two stimuli appeared

287   at a different location. The tactile locations on the other task-irrelevant hand were

288   selected in the same way for each tactile test set (50% match and mismatch trials for

289   S1 items presented to the irrelevant hand). Matches and mismatches on the attended

290   and unattended hands were uncorrelated. In unimodal blocks, only visual memory test

291   displays were presented, and participants could therefore ignore the tactile stimuli that

292   appeared concurrently with visual S1 displays. Experiment 1a included 12 blocks with

293   48 trials per block (576 trials in total, 144 trials for each of the four combinations of

294   stay/shift trials and unimodal/bimodal blocks). The unimodal and bimodal WM tasks

295   were performed in six successive blocks, with task order counterbalanced across

296   participants.

297   ------------------------------

298   insert Figure 1 about here

299   ------------------------------

300

301   **Experiment 1b** Touch was the primary modality, vision was the secondary modality.

302   Tactile targets were defined by stimulus waveform (counterbalanced across

303   participants, continuous: 200 ms vibration, or pulsed: two 10 ms pulses followed by

304   two 10 ms pulses after a 160 ms gap). Two tactile sample sets (S1 and S2) were

305   presented on each trial. S1 included two tactile stimuli (one continuous, one pulsed),

306   each delivered to a randomly selected finger of each hand. At S2, two different fingers

307   of each hand were stimulated. One hand received a pair of pulsed stimuli, the other a

308   pair of continuous stimuli). In stay trials, all continuous and all pulsed tactile S1 and

309   S2 stimuli were presented to the same hand. In shift trials, continuous and pulsed

310   stimuli swapped sides between S1 and S2, so that the to-be-memorized tactile stimuli

311   were presented to opposite hands. Bilateral visual sample stimuli (identical to

312   Experiment 1a) were presented simultaneously with the tactile S1 sets. No visual

313   samples appeared at S2. In bimodal blocks, participants memorized all tactile S1 and

314   S2 targets, as well as the visual S1 stimuli that were located on the same side as the

315   tactile S1 targets. Memory was unpredictably tested for touch or vision. Visual memory

316   test sets were identical to the sample sets, except that on mismatch trials (50%), one

317   of the sample colors on the task-relevant side was replaced by a different color. Tactile

318   memory test sets included one continuous and one pulsed stimulus, delivered to

319   different hands. Participants had to decide whether the location of the task-relevant

320   (continuous or pulsed) tactile test stimulus matched the location of one of the three

321   task-relevant tactile sample stimuli (match trials, 50%) or was presented at a different

322   location (mismatch trials, 50%). In unimodal blocks, only touch was tested, and visual

323   S1 stimuli could be ignored.

324   Experiment 1b included 12 blocks with 48 trials per block (576 trials in total, 144

325   trials for each of the four combinations of stay/shift trials and unimodal/bimodal

326   blocks). The unimodal and bimodal WM tasks were performed in six successive

327   blocks, counterbalanced across participants. Two procedural changes relative to

328   Experiment 1a were introduced for pragmatic reasons. First, participants memorized

329   two visual targets at S1 and S2, while in Experiment 1b, they had to memorize one

330   tactile S1 and two tactile S2 targets. This was necessitated by the fact that there were

331   only four tactile stimulus locations for each hand, and that a tactile WM load of two

332   items for S1 and S2 would have resulted in all four fingers of the same hand receiving

333   a target stimulus on stay trials. Second, the locations of visual S1 targets varied

334   unpredictably across trials in Experiment 1a, whereas the location of tactile S1 targets

335   (and thus the location of visual targets in bimodal blocks) remained constant in each

336   block in Experiment 1b, and was changed every three blocks (with the task-relevant

337   side for the first block having been randomly determined per participant). This was

338   done because pilot data indicated that a trial-wise randomization of tactile S1 target

339   locations would have resulted in an extremely challenging task. Critically for the

340   purposes of the present study, the location of tactile S2 targets (same versus opposite

341   side) remained entirely unpredictable.

342

343   **Experiment 2**

344   Participants concurrently performed sequential loading tasks in both modalities,

345   with bimodal S1 and S2 sets followed unpredictably by a unimodal tactile or visual test

346   set. As in Experiment 1b, the task-relevant tactile and visual S1 targets were located

347   on the same side (left or right), and this location remained constant within each block,

348   and was changed every three blocks. Critically, the locations of the task-relevant visual

349   and tactile sample stimuli in S2 were orthogonally randomized for each modality (stay

350   vs. shift, 50%), resulting in the need to shift attention in the period after S2 in neither

351   modality (25%), in only one modality (touch or vision, 25% each), or in both modalities

352   simultaneously (25%). In contrast to Experiment 1, where participants had to retain

353   the colors of visual samples and the locations of tactile samples, they memorized

354   stimulus locations for both modalities in Experiment 2. This change was introduced

355   because a common representational format for stimuli in different modalities has been

356   reported to produce crossmodal interference in previous auditory-visual WM tasks

357   (see Exp. 8 in Fougnie et al. 2015).

358   Each visual sample set included pairs of two green and two red circles (stimulus

359   size: 0.40° of visual angle) on opposite sides. These stimuli were presented on two

360   virtual (invisible) concentric rings around the fixation dot (radius relative to fixation:

361   1.86° and 1.29° for the outer and inner rings). All four stimuli in each sample display

362   appeared at the same eccentricity. On trials where S1 items were located in the inner

363   ring, S2 items were located on the outer ring, or vice versa; see Figure 1. Stimulus

364   locations were randomly sampled from 140 angular positions (in polar coordinates:

365   110° to 250° for the left side, 290° to 70° for the right side) with the constraint that the

366   stimulus pairs on each side of the sample displays were separated by a minimum

367   distance of 80°. To-be-memorized visual target stimuli were defined by their color

368   (green or red, counterbalanced across participants). Participants now had to memorize

369   the locations of the task-relevant visual sample stimuli in S1 and 2. Visual memory test

370   displays contained one green and one red circle on opposite sides. Participants had

371   to decide whether the location of the target-color test item matched the location of one

372   of the visual target items in S1 and S2. This was the case in half of all trials where

373   visual WM was tested. In the remaining 50% mismatch trials, the target-color item in

374   the test display appeared at a different location, at an angular distance of 40° relative

375   one of the memorized locations in S1 or S2.

376   Tactile sample and test stimuli were identical to those used in Experiment 1b

377   (tactile targets: continuous or pulsed, counterbalanced across participants), with the

378   exception that only a single task-relevant tactile item was presented both at S1 and

379   S2. Each tactile sample set included a target and a distractor stimulus, presented to

380   opposite hands.S2 samples were never presented to any location stimulated at S1.

381   The task-relevant tactile stimulus in the test set either matched the location of one of

382   the two tactile targets in S1 or S2, or was presented to a non-target location (50%

383   match/mismatch). Experiment 2 included 16 blocks with 34 trials per block (544 trials

384   in total; 136 trials for each of the four combinations of tactile stay/shift and visual

385   stay/shift trials). The task-relevant side for S1 was randomly determined for block 1,

386   and changed to the opposite side in block 9.

387

Analysis of EEG data

389   **Acquisition and pre-processing** EEG data, sampled at 500 Hz using a BrainVision

390   amplifier, were DC-recorded from 64 Ag/AgCl active electrodes at standard locations

391   of the extended 10-20 system. Two electrodes at the outer canthi of the eyes

392   monitored horizontal eye movements (horizontal electrooculogram, HEOG).

393 Continuous EEG data were referenced to the left mastoid during recording, and re-

394 referenced to the arithmetic mean of both mastoids for data pre-processing. Data were

395 offline low-pass filtered (20 Hz, Blackman window, filter order 1000). All EEG results

396 reported below were virtually identical when a higher low-pass cut-off of 40 Hz was

397 employed. Epochs were extracted for the 2s period after the sample set, and were

398 corrected relative to a 200 ms pre-stimulus baseline.

399

400 **Artefact rejection and correction** We first rejected trials with saccades using a

401 differential step function that ran on the bipolarized HEOG (step width 100 ms,

402 threshold 30 µV) prior to artefact correction. *Independent Component Analysis* (ICA)

403 (Delorme, Sejnowski, Makeig 2007) was employed to correct for frontal artefacts such

404 as eye blinks, and residual traces of horizontal eye movements that had not been

405 detected by the step function. We further rejected trials in which difference values for

406 corresponding left- minus right-hemispheric electrodes, averaged between 300 and

407 2000 ms after S1, exceeded a fixed threshold of ± 80 µV (for any electrode pair), as

408 well as trials where difference values exceeded ± 4 standard deviations per individual

409 dataset (for at least two electrode pairs). The remaining EEG epochs entered *Fully*

410 *Automated Statistical Thresholding for EEG Artifact Rejection* (FASTER, Nolan,

411 Whelan, Reilly 2010) for the interpolation of noisy electrodes, and were subsequently

412 converted to current source densities (CSDs: iterations = 50, m = 4, lambda = 10^{-5};

413 Tenke and Kayser 2012). 93.4% of all epochs were retained for analysis after artifact

414 rejection (Experiment 1a: 92.9%, Experiment 1b: 93.2%, Experiment 2: 93.8%).

415 Statistical tests were based on correct and incorrect trials, since the exclusion of

416 incorrect trials did not change the pattern of results, but would have reduced the signal-

417 to-noise ratio of EEG data.

418

419 **Electrodes and EEG analyses** CSDs were separately averaged across three

420 adjacent electrode pairs contralateral and ipsilateral to the task-relevant side. Tactile

421 contralateral delay activity (tCDA component) was measured at lateral central scalp

422 regions (C3/4, FC3/4, CP3/4), and visual contralateral delay activity (CDA) was

423 measured at lateral occipital regions (PO7/8, PO3/4, O1/2). The electrode locations

424 used to quantify tCDA and CDA components were identical to those employed in

425 previous studies (Katus and Eimer 2016; Katus, Grubert, and Eimer 2017; Katus and

426 Eimer 2018a; 2018b). Separate CDA/tCDA components were computed for the delay

427 periods following the two sample sets (S1 and S2), based on averaged CSDs obtained

428 between 300 and 1000 ms following the onset of S1 or S2 (e.g., Katus and 2015; Vogel

429 and Machizawa 2004). Statistical tests of neural activity during these periods were

430 conducted on difference values of contra- minus ipsilateral CSDs. Error bars in graphs

431 indicate 95% confidence intervals (CIs) for the true population mean. Thus, error bars

432 that do not overlap with the zero axis ($y \neq 0$) indicate statistical significance of

433 tCDA/CDA components; error bars that do not overlap with chance level ($y \neq 50\%$)

434 indicate behavioral performance that is significantly above chance.

435   Spline-interpolated topographical voltage maps were computed as follows:

436 First, we averaged CSD amplitudes for the time windows of interest. These data were

437 collapsed across trials with left and right S1 targets by flipping electrode coordinates

438 over the midline for trials with left-side S1 targets. Trials were then averaged

439 separately for each experimental condition. To calculate contra-/ipsilateral difference

440 values, we used a copy of the data, and after flipping electrode coordinates over the

441 midline, we subtracted this inverted copy from the original data. This procedure

442 eliminates any non-lateralized activity, thereby revealing lateralized effects that reflect

443 amplitude differences between corresponding left- vs. right-hemisphere electrodes.

444 Note that the resulting full topographical maps are essentially equivalent to maps

445 where the inverse of the contra-ipsilateral amplitude difference measured over one

446 hemisphere is projected to the other hemisphere. As a result, these full topographic

447 maps show a symmetrical distribution of lateralized activity, which enhances the

448 visibility of tCDA and CDA components, and highlights the fact that the polarity of these

449 components can vary independently. In these maps, tCDA/CDA components evoked

450 by the S1 targets appear as negativity over the left hemisphere, and tCDA/CDA

451 polarity reversals during the period following S2 as a positivity over the left hemisphere

452 (i.e., a negativity over the right hemisphere).

453

454 **Bayes factor analysis** Conventional null-hypothesis significance tests can provide

455 evidence against the null hypothesis, but cannot confirm the null hypothesis for a

456 particular effect or interaction. We calculated Bayes factors using Bayesian t-tests

457 (Rouder et al. 2009) and the software Jasp (JASP team 2016) to formally decide

458 between the alternative and null hypotheses (i.e., presence vs. absence of a

459 modulation) for each main effect / interaction in our statistical designs. The Bayes

460 factor for the null-hypothesis (BF_{01}) corresponds to the inverse of the Bayes factor for

461 the alternative hypothesis (BF_{10}), and indexes the relative evidence in the data for the

462 absence rather than presence of a statistical difference. We always report the

463 numerically larger BF. Reliable evidence for either hypothesis is marked by a BF > 3

464 (Jeffreys 1961), suggesting that the empirical data are at least 3 times more likely

465 under this hypothesis as compared to the competing hypothesis.

466

467

Results

Experiment 1a

Figure 2 displays CSDs recorded over visual and somatosensory brain areas contralateral and ipsilateral to task-relevant S1 items in Experiment 1a, where vision and touch were the primary and secondary modality, respectively. The corresponding contralateral-ipsilateral difference waves are shown in Figure 3a. As illustrated in the left panels of Figure 2, the maintenance of visual sample stimuli in WM elicited visual CDA components in all experimental conditions[1]. As predicted, the CDA reversed polarity during the delay period following S2 on shift trials but not on stay trials. Importantly, this CDA polarity reversal was very similar in unimodal blocks and in bimodal blocks where tactile stimuli from the S1 set had to be maintained concurrently; see Figure 3a. A somatosensory tCDA component was elicited during the maintenance of these stimuli in the S1 and S2 delay periods in bimodal blocks but was absent in unimodal blocks. In the period following S2, tCDA components were essentially unaffected by whether and attention shift was required in response to S2 in the visual modality; Figure 3a.

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insert Figure 2 about here

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[1] Unless explicitly stated otherwise, all tCDA/CDA components reported in this article were statistically significant, as confirmed by t-tests of contra/ipsi difference values against zero. The reliable presence of these components is shown in Figures 3 and 7, where statistically reliable modulations are indicated by error bars that do not overlap with the zero-axis (see Methods for further details).

488 **Primary modality (Vision, CDA components).** CSD values obtained during the

489 delay period following S2 were analyzed by separate ANOVAs with the factors *Task*

490 *type* (unimodal vs. bimodal) and *Trial type* (stay vs. shift). Because stay versus shift

491 trials only differed with respect to the side where visual S2 targets were presented,

492 these trials were collapsed for the analysis of CDAs during the S1-period. CDA

493 amplitudes were reduced in the bimodal task where both tactile and visual S1 targets

494 had to be maintained relative to the unimodal task where touch was irrelevant. These

495 bimodal costs for CDA amplitudes were present both during the S1-period (*Task type*:

496 $t(11) = 3.900$, $p = 0.003$, $BF_{10} = 18.689$) and during the S2-period (*Task type*: $F(1,11)$

497 $= 9.859$, $p = 0.009$, $BF_{10} = 6.217$). CDA components reversed polarity during the S2-

498 period on shift trials but not on stay trials (*Trial type*: $F(1,11) = 35.986$, $p = 10^{-4}$, BF_{10}

499 $= 317.813$). Importantly, the size of this CDA difference between stay and shift trials

500 was identical in unimodal and bimodal blocks (*Task type* x *Trial type*: $F(1,11) = 0.067$,

501 $p = 0.800$, $BF_{01} = 3.379$); see Figure 3, left side.

502 A follow-up ANOVA tested whether the reduction of CDA amplitudes in bimodal

503 as compared to unimodal blocks, which was already present in the S1-period, might

504 have obscured any interaction between *Task type* and *Trial type* in the S2-period. To

505 eliminate any effects associated with CDA amplitude differences during the first delay

506 period, we used the full S1-period as a new baseline, by subtracting CDA amplitudes

507 measured in the S1-period from those measured after S2. This subtraction eliminated

508 the *Task type* main effect ($F(1,11) = 0.070$, $p = 0.796$, $BF_{01} = 3.375$) and increased the

509 *Trial type* effect ($F(1,11) = 48.031$, $p < 10^{-4}$, $BF_{10} = 970.181$) for CDAs during the S2-

510 period. Critically, there was still no interaction between these two factors (*Task type* x

511 *Trial type*: $F(1,11) = 0.009$, $p = 0.926$, $BF_{01} = 3.466$). These results demonstrate that

512   the sustained maintenance of tactile information on one side in bimodal blocks had no

513   effect on the polarity shift of visual CDA components on switch versus stay trials.

514

515   **Secondary modality (Touch, tCDA component)** The tCDA was analyzed in the

516   same fashion as the CDA (see above). A reliable tCDA component was elicited during

517   the S1-period in the bimodal task ($t(11) = 5.590$, $p < 10^{-3}$, $BF_{10} = 189.203$), but not in

518   the unimodal task ($t(11) = 0.656$, $p = 0.526$, $BF_{01} = 2.894$; main effect of *Task type*:

519   $t(11) = 5.114$, $p < 10^{-3}$, $BF_{10} = 101.232$). This tCDA difference between the bimodal

520   and unimodal tasks persisted during the S2-period (*Task type:* $F(1,11) = 12.237$, $p =$

521   0.005, $BF_{10} = 10.456$). There were no other significant effects in the S2-period (*Trial*

522   *type*: $F(1,11) = 1.816$, $p = 0.205$, $BF_{01} = 1.670$; *Trial type* x *Task type*: $F(1,11) = 0.336$,

523   $p = 0.574$, $BF_{01} = 3.012$). In bimodal blocks, tCDA amplitudes during the S2-period did

524   not significantly differ between visual stay and shift trials ($t(11) = 0.602$, $p = 0.560$,

525   $BF_{01} = 2.978$). This result did not change after subtracting an S1-period baseline from

526   tCDA amplitudes in the S2-period ($t(11) = 0.163$, $p = 0.874$, $BF_{01} = 3.440$), indicating

527   that attention shifts in the primary visual modality did not affect concurrent tactile WM

528   maintenance processes.

529

530   -----------------------------

531   insert Figure 3 about here

532   -----------------------------

533

534   **Behavioral data** Participants responded correctly in 85.1% of trials when memory was

535   tested for the primary modality (vision). The accuracy on trials in the bimodal WM task

536   where memory was tested for touch was 87.9%. Accuracy for the visual WM task was

537   reduced in bimodal relative to unimodal blocks (83.2% vs. 87.0% correct; *Task type*:

538   F(1, 11) = 18.076, p = 0.001, BF_{10} = 30.861); see Figure 4A. There were no other

539   significant effects or interactions for visual WM performance (*Trial type* x *Task type*:

540   F(1, 11) = 0.311, p = 0.588, BF_{01} = 3.044; *Trial type:* F(1, 11) = 0.991, p = 0.341, BF_{01}

541   = 2.299). Accuracy for the tactile WM task in bimodal blocks was not significantly

542   reduced in visual shift as compared to stay trials (86.4% vs. 89.4% correct; *Trial type*:

543   t(11) = 1.979, p = 0.073, BF_{10} = 1.242).

544

545   ------------------------------

546   insert Figure 4 about here

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548

549   **Experiment 1b**

550   In Experiment 1b, touch was the primary and vision secondary modality. Tactile and

551   visual CDA components elicited by tactile and visual sample stimuli are shown in

552   Figure 5, and the corresponding difference waveforms are displayed in Figure 3B. The

553   pattern of CDA modulations observed for the primary and secondary modalities were

554   very similar to the results of Experiment 1a; see Figure 2. For the primary tactile WM

555   task, tCDA components reversed polarity in the S2-period on tactile shift trials, and

556   this was the case not only in unimodal but also in bimodal blocks. Visual sample stimuli

557   at S1 triggered CDA components in the bimodal task but not in the unimodal task when

558   they were irrelevant. Importantly, visual CDAs observed during the S2-period in

559   bimodal blocks did not change polarity on tactile shift trials.

560

561

562   ------------------------------

563   insert Figure 5 about here

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565

566   **Primary modality (Touch, tCDA components)** CSD values obtained during the

567   delay periods following S1 and S2 were analyzed with the same statistical tests as in

568   Experiment 1a. The amplitudes of tCDA components were reduced in bimodal as

569   compared to unimodal blocks during the S1-period (*Task type*: $t(15) = 2.801$, $p = 0.013$,

570    $BF_{10} = 4.293$), as was found for the visual CDA in Experiment 1a. However, this tCDA

571   amplitude difference between the two tasks was no longer present during the S2-

572   period *(Task type*: $F(1,15) = 0.006$, $p = 0.939$, $BF_{01} = 3.904$). As predicted, the tCDA

573   reversed its polarity during the S2-period on tactile shift trials but not on tactile stay

574   trials (*Trial type*: $F(1,15) = 54.076$, $p < 10^{-5}$, $BF_{10} > 10^3$). Critically, there was no *Task*

575   *type* x *Trial type* interaction ($F(1,15) = 0.016$, $p = 0.900$, $BF_{01} = 3.887$), demonstrating

576   that this tCDA polarity reversal did not differ between the bimodal task where visual

577   S1 sample stimuli on one side had to be maintained throughout, and the unimodal task

578   where visual samples could be ignored; see Figures 3B and 5.

579   These results were confirmed in a control analysis, where the S1-period

580   baseline was subtracted from activity in the S2-period, as in Experiment 1a. There was

581   a main effect for *Trial type* ($F(1,15) = 60.670$, $p < 10^{-5}$, $BF_{10} > 10^4$), no significant effect

582   for *Task type* ($F(1,15) = 4.293$, $p = 0.056$, $BF_{10} = 1.379$), and importantly, no interaction

583   between both factors (*Trial type* x *Task type*: $F(1,15) = 0.034$, $p = 0.856$, $BF_{01} = 3.856$).

584

585

Secondary modality (Vision, CDA components) During the S1-period, reliable CDA components only emerged in the bimodal task ($t(15) = 6.133$, $p < 10^{-4}$, $BF_{10} > 10^3$), but not in the unimodal task where visual sample stimuli were irrelevant ($t(15) = 1.395$, $p = 0.183$, $BF_{01} = 1.730$), and this difference was significant (*Task type*: $t(15) = 6.098$, $p < 10^{-4}$, $BF_{10} > 10^3$). This CDA difference between the two tasks remained present during the S2-period (*Task type:* $F(1,15) = 12.237$, $p = 0.005$, $BF_{10} = 10.456$). There were no other significant effects for CDA amplitudes during the S2-period (*Trial type*: $F(1,15) = 1.816$, $p = 0.205$, $BF_{01} = 1.670$; *Trial type* x *Task type*: $F(1,15) = 0.336$, $p = 0.574$, $BF_{01} = 3.012$). Importantly, CDA amplitudes measured in the bimodal task did not differ between tactile stay versus shift trials ($t(15) = 0.647$, $p = 0.527$, $BF_{01} = 3.256$), and this pattern did not change when an S1-period baseline was subtracted from the CDA ($t(15) = 0.093$, $p = 0.927$, $BF_{01} = 3.900$).

Behavioral data Observers responded correctly in 90.3% of all trials in which memory was tested for the primary modality (touch), and in 92.4% of bimodal trials where memory was tested for vision; see Figure 4A. Tactile WM accuracy was reduced in bimodal relative to unimodal blocks (87.2% vs. 90.3% correct; *Task type*: $F(1,15) = 8.219$, $p = 0.012$, $BF_{10} = 4.786$). Performance in response to tactile test stimuli was worse in tactile shift versus stay trials (84.5% vs. 93.0% correct; *Trial type*: $F(1, 15) = 18.030$, $p = 0.001$, $BF_{10} = 51.782$), demonstrating that participants found it more difficult to retain the locations of tactile samples presented successively to different hands. However, there was no *Task type* x *Trial type* interaction ($F(1, 15) = 0.976$, $p = 0.339$, $BF_{01} = 2.568$), indicating that performance costs on tactile shift trials were equally present in unimodal and bimodal blocks, und were thus unrelated to the additional requirement to maintain visual sample stimuli on one side. WM accuracy for

611 vision as secondary modality in the bimodal task did not differ between tactile shift and

612 stay trials (92.3% vs. 92.6%; *Trial type*: t(15) = 0.235, p = 0.818, BF_{01} = 3.8201).

613

614

615 **Experiment 2**

616 To further scrutinize the apparent independence of the space-based attentional control

617 of visual and tactile WM maintenance, Experiment 2 employed an orthogonal design

618 where the presence versus absence of shifts between the task-relevant tactile or visual

619 samples at S1 and S2 was manipulated independently for each modality. In addition,

620 the visual WM task was changed relative to Experiment 1. As was the case for the

621 tactile WM task, it now also involved the retention of spatial locations (see Figure 1C).

622 In Experiment 2, there were no unimodal blocks, and no distinction between primary

623 and secondary modalities. On all trials, bimodal visual/tactile sample sets were

624 presented at S1 and S2, and participants had to memorize task-relevant sample items

625 on one side for each sample set. The visual and tactile S1 targets were always located

626 on the same side, and this side remained constant within blocks. Visual and tactile S2

627 targets could appear on the same side or on the opposite side, and this was

628 manipulated independently, resulting in four trial types (vision & touch stay; vision &

629 touch shift; vision stay / touch shift; vision shift / touch stay).

630

631 -----------------------------

632 insert Figure 6 about here

633 -----------------------------

634

Visual and somatosensory delay activity (CDA/tCDA) Tactile and visual CDA components entered the same ANOVA, with *Component* (tCDA: CSD values at C3/4, FC3/4, CP3/4; CDA: CSD values at PO7/8, PO3/4, O1/2) included as a separate factor. Because the CDA and CDA components index modality-specific WM maintenance processes (Katus and Eimer 2016), the difference between visual stay and shift trials should primarily affect the visual CDA during the S2-period (*Tracked Trial type,* TT: stay vs. shift), but not the somatosensory tCDA (*Untracked Trial type,* UT: stay vs. shift). Analogously, the difference between tactile stay and shift trials should primarily affect the tCDA, but not the CDA component during the S2-period. The data shown in Figure 6 and the corresponding difference waveforms shown in Figure 7 are in line with this prediction. CDA components changed polarity on visual shift trials, but were unaffected by whether the side of tactile target samples remained the same or shifted between S1 and S2. For tCDA components, there was a polarity reversal on tactile shift trials, but no difference between visual shift and stay trials.

In all four conditions of Experiment 2, and during both the S1- and S2-periods, reliable lateralized activity was present over visual and somatosensory cortex, as indicated by the error bars of contra-/ipsilateral difference values shown in Figure 7. Difference values obtained during the S1- and S2-periods were submitted to separate three-way ANOVAs with the factors TT (stay/shift), UT (stay/shift) and *Component* (tCDA/CDA). Since the locations of the tactile/visual S2 targets was unpredictable in all trials, there should be no significant effects for the factors TT / UT during the S1-period, and this was confirmed (TT: $F(1,15) = 0.005$, $p = 0.944$, $BF_{01} = 3.906$; UT: $F(1,15) = 0.027$, $p = 0.871$, $BF_{01} = 3.868$; *Component* x TT: $F(1,15) = 0.572$, $p = 0.461$, $BF_{01} = 3.048$; *Component* x UT: $F(1,15) = 0.075$, $p = 0.787$, $BF_{01} = 3.787$; TT x UT: $F(1,15) = 1.976$, $p = 0.180$, $BF_{01} = 1.710$; *Component* x TT x UT*: $F(1,15) = 0.101$, $p =$

660 0.755, BF_{01} = 3.743). There was a main effect of *Component* during the S1-period

661 (F(1,15) = 5.254, p= 0.037, BF_{10} = 1.911), reflecting the known fact that CDA

662 amplitudes were generally larger than tCDA amplitudes (e.g., Katus and Eimer 2018a).

663   During the S2-period, a main effect of *Tracked Trial type* (TT: F(1,15) = 42.116,

664 p < 10^{-5}, BF_{10} > 10^4) was present, reflecting a polarity reversal of the visual CDA

665 component on visual shift trials, and of tactile CDA components on tactile shift trials;

666 see Figures 6 and 7. Critically, there was no main effects or interactions involving the

667 factor *Untracked Trial type* (UT: F(1,15) = 0.058, p = 0.813, BF_{01} = 3.815; TT x UT:

668 F(1,15) = 0.230, p = 0.638, BF_{01} = 3.536; *Component* x UT: F(1,15) = 1.033, p = 0.326,

669 BF_{01} = 2.507; *Component* x TT x UT: F(1,15) = 0.119, p = 0.735, BF_{01} = 3.713). This

670 demonstrates that the visual CDA was unaffected by the presence or absence of shifts

671 in touch, and that the tactile CDA was not sensitive to the difference between visual

672 stay versus switch trials. There was no significant main effect of *Component* in the S2-

673 period (F(1,15) = 0.873, p = 0.365, BF_{01} = 2.681), but there was an interaction between

674 *Component* and TT (F(1,15) = 9.755, p = 0.007, BF_{10} = 7.370). This interaction reflects

675 the fact that CDA amplitude differences between visual stay versus shift trials were

676 larger than the corresponding tCDA amplitude differences between tactile stay and

677 shift trials); note the different scales for tCDA/CDA components in Figure 7. Due to the

678 absence of any differential effects of TT or UT during the S1-period in Experiment 2

679 (see above), no additional control analyses with S1-period baselines were conducted

680 for CDA amplitudes following S2.

681 ------------------------------

682 insert Figure 7 about here

683 ------------------------------

Behavioral data Participants responded correctly in 78.5% of all trials. The percentage of correct responses entered an ANOVA with the factors *Tested modality Trial type* (TT: stay/shift), *Untested modality Trial type* (UT: stay/shift) and *Tested modality* (vision or touch). Accuracy was higher when touch was tested than when vision was tested (82.6% vs. 74.5%; *Tested modality*: $F(1,15) = 7.362$, $p = 0.016$, $BF_{10} = 3.717$), reflecting the lower WM load for the tactile task (1 target item per sample set) than for the visual task (2 targets per set). WM performance for the tested modality tended to be worse on shift trials relative to stay trials, but this reduction was not significant (TT: $F(1,15) = 3.778$, $p = 0.071$, $BF_{10} = 1.150$). Importantly, accuracy in the tested modality was unaffected by the presence versus absence of a location shift for relevant sample items in the untested modality (UT: $F(1,15) = 0.091$, $p = 0.767$, $BF_{01} = 3.760$). There was also no interaction between stay/shift trials in the tested and untested modalities (TT x UT: $F(1,15) = 0.196$, $p = 0.665$, $BF_{01} = 3.589$). Further effects were non-significant (TT x UT x *Tested modality*: $F(1,15) = 0.042$, $p = 0.841$, $BF_{01} = 3.842$; TT x *Tested modality*: $F(1,15) = 2.702$, $p = 0.121$, $BF_{01} = 1.292$; UT x *Tested modality*: $F(1,15) = 1.308$, $p = 0.271$, $BF_{01} = 2.237$).

To test whether the presence versus absence of attention shifts in the tested or untested modality during the S2-period selectively affected the retention of S2 sample stimuli that had to be encoded in this period, additional analyses of WM accuracy were conducted only for trials where memory was tested for S2 stimuli, separately for hit rates (from match trials) and correct rejection rates (from mismatch trials). These analyses involved the factors *Tested modality* (touch or vision), *Tested modality Trial type* (TT: stay or shift) and *Untested modality Trial type* (UT: stay or shift). For hit rates, accuracy was again higher for tactile as compared to visual memory probes ($F(1, 15) = 11.657$, $p = 0.004$, $BF_{10} = 12.142$). There were no significant effects or interactions

709   involving TT or UT (all ps > 0.05), indicating that attention shifts in either modality had

710   no impact on memory for S2 items. For correct rejection rates, no significant effects

711   were found (ps > 0.05).

712

713

714   Discussion

715   To examine the flexibility of space-based attentional control mechanisms in

716   multimodal WM, we employed sequential loading procedures in bimodal visual/tactile

717   WM tasks, and measured visual and tactile CDA components as ERP markers of the

718   attentional activation of WM representations in modality-specific visual and

719   somatosensory brain regions. On each trial, two memory sample sets (S1/S2) were

720   presented sequentially, and the critical manipulation was whether the S1 and S2

721   targets in a given modality were located on the same side or on opposite sides (stay

722   vs. shift trials).

723   Experiment 1 included unimodal baseline conditions where only primary-

724   modality stimuli (vision in Exp.1a, touch in Exp.1b) were task-relevant and S1 sample

725   sets in the other modality could be ignored. In these unimodal WM tasks, visual and

726   tactile CDA components were elicited contralateral to S1 targets in the S1-period and

727   then reversed polarity during the S2-period on shift trials. This confirms previous

728   observations from unimodal tactile and visual sequential loading experiments (Katus

729   and Eimer 2015; Berggren and Eimer 2016), and indicates that spatial attention was

730   reallocated to the location of S2 targets during the second delay period. In these two

731   unimodal baseline tasks, there were no reliable CDA components over visual areas in

732   blocks where visual sample stimuli had be ignored, and no significant tCDA

components over somatosensory areas in blocks were tactile samples were irrelevant. These observations show that the presence of these components was determined by the task-relevance of the corresponding sensory modality. This also demonstrates the feasibility of our CDA/tCDA co-registration methods using CSDs in preventing any carryover of lateralized ERP effects from visual to somatosensory areas, or vice versa (see also Katus and Eimer, 2016; Katus, Grubert, Eimer 2017; Katus and Eimer, 2018a; 2018b; for additional evidence for the separability of CDA and tCDA components in bimodal visual/tactile WM tasks).

The critical question addressed in Experiment 1 was whether there would be any spatial synergies between space-based attentional control processes in bimodal visual/tactile blocks where sample stimuli from both modalities had to be maintained. In Experiment 1a, vision was the primary modality. There were visual stay and shift trials, and observers also had to maintain tactile S1 targets throughout the delay periods following S1 and S2. The visual CDA initially emerged over the hemisphere contralateral to visual S1 targets, and reversed polarity on shift trials when visual S2 targets were presented on the opposite side. Crucially, this CDA polarity reversal was identical in unimodal and bimodal blocks, and Bayesian tests confirmed the absence of Trial Type x Block Type interactions in the S2-period. Thus, having to maintain a sustained attentional focus on one side in tactile WM had no effect on the execution of spatial attention shifts in visual WM towards S2 targets on shift trials. Exactly the same pattern of CDA results was observed in Experiment 1b, where the roles of vison and touch as primary and secondary modalities were reversed. Here, tactile CDA components reversed polarity on shift trials, and this polarity reversal was identical in unimodal and visual blocks. In addition, and importantly, having to re-allocate attention to the opposite side versus maintaining attention on the same side in the

758   primary modality had no impact on the polarity and amplitudes of CDA components

759   for the secondary modality (touch in Exp 1a, vision in Exp 1b). This demonstrates that

760   the constant focus of spatial attention during the maintenance of WM representations

761   in the secondary modality remained unaffected by the presence versus absence of

762   attention shifts during the S2-period in the primary WM task.

763   In line with this apparent independence of space-based attentional control

764   mechanisms in visual and tactile WM, there were also no differences in WM

765   performance between bimodal shift and stay trials in Experiment 1. In particular,

766   accuracy on trials where WM for the secondary modality was tested was unaffected

767   by whether primary modality S1 and S2 targets were presented on the same or on

768   opposite sides. In other words, the maintenance of tactile or visual S1 samples was

769   not impaired when the attentional focus in the other modality had to be re-allocated to

770   the opposite side during the S2-period.

771   There was however a general bimodal cost for WM performance in Experiment

772   1. Accuracy for the WM task in the primary modality was higher in unimodal baseline

773   blocks relative to bimodal blocks, and this was the case both for vision in Exp.1a and

774   for touch in Exp.1b. These bimodal performance costs are in line with observations

775   from previous behavioral studies (e.g., Fougnie and Marois 2011; Saults and Cowan

776   2007), and they were accompanied by corresponding CDA differences between

777   unimodal and bimodal blocks. Visual and tactile CDA/tCDA amplitudes for the primary

778   tasks in Experiments 1a and 1b were smaller in bimodal blocks where secondary

779   modality sample items had to be maintained concurrently relative to unimodal blocks

780   where these items could be ignored (Task Type main effect). These findings are

781   consistent with a previous EEG experiment (Katus and Eimer 2018b) where CDA

782   amplitudes elicited during visual WM maintenance were generally smaller when this

783   task was performed concurrently with a tactile WM task, relative to a single-task

784   baseline condition. This CDA attenuation in the bimodal task was interpreted as a

785   result of the increased demands on central executive dual-task coordination

786   mechanisms, and thus as a limitation in the concurrent top-down control of multiple

787   WM maintenance processes in different modalities. Importantly, dual-tasking

788   attenuated visual CDA amplitudes by the same amount regardless of WM load in the

789   visual task, and visual load had no impact on tactile CDA amplitudes elicited during

790   the maintenance of tactile items in the bimodal task. These observations suggest that

791   these bimodal costs are unrelated to the capacity of sensory storage mechanisms (see

792   Katus and Eimer 2018b, for further discussion). To eliminate amplitude differences

793   between bimodal and unimodal task conditions during the S1-period, we ran additional

794   analyses of tCDA/CDA components elicited in the S2-period after subtracting out

795   tCDA/CDA amplitudes in the S1-period. This new baseline confirmed the absence of

796   any Task Type x Trial Type interactions in Experiments 1a and 1b, as indicated by

797   Bayesian analyses for both experiments. This result further underlines the

798   independence of modality-specificity attentional control processes in visual and tactile

799   WM, and demonstrates that this independence was unrelated to the dual-task

800   coordination costs that accounted for reduced tCDA/CDA amplitudes in bimodal

801   blocks during the S1-period.

802   In Experiment 1, attention shifts in the primary modality that took place during

803   the S1-period had no impact on the stable focus of attention within the secondary

804   modality that was already established during the S1-period. In Experiment 2, the

805   necessity to shift attention between S1 and S2 or to maintain an attentional focus on

806   the same side was orthogonally manipulated for visual and tactile WM, resulting in

807   trials requiring attention shifts in one modality, neither modality, or in both modalities

808   simultaneously. In contrast to Experiment 1, where participants memorized colors for

809   the visual task and locations for the tactile tasks, memory for spatial locations was

810   required for both tasks in Experiment 2. This change was introduced to maximize the

811   representational overlap between both modalities (see Tamber-Rosenau and Marois

812   2016, Exp. 8 in Fougnie et al. 2015), and to test whether the independent attentional

813   control of visual and tactile WM found in Experiment 1 was linked to the fact that

814   different types of information (spatial vs. featural) had to be maintained in different

815   modalities (cf., Zimmer 2008). As in Experiment 1, visual CDA and CDA components

816   initially emerged contralateral to the S1 targets. During the S2-period, the polarity of

817   these CDA components was determined exclusively by the location of S2 target

818   sample items in the corresponding modality, and was entirely unaffected by whether

819   targets in the other untracked modality required a shift of spatial attention or not; see

820   Figure 6. The polarity of the visual and tactile CDAs reversed on visual or tactile shift

821   trials but not on visual or tactile stay trials, respectively (TT: Tracked Trial type main

822   effect; see topographical maps in Figure 7). Crucially, whether an attention shift was

823   or was not required within one modality during the S2-period had no impact on the

824   amplitudes of CDA components associated with the other modality (UT: Untracked

825   Trial type main effect). There was also no evidence for any interactions between these

826   two factors.

827   The behavioral results of Experiment 2 also demonstrated that WM

828   maintenance in vision and touch was not affected by the spatial relationship between

829   S1 and S2 targets in the other modality. WM accuracy for the modality that was tested

830   did not differ between trials with versus without a location shift of S1 and S2 targets in

831   the other untested modality. The reliability of all critical null effects for CDA/tCDA

832   amplitudes and WM performance was confirmed with Bayesian tests. Overall, these

833 results of Experiment 2 provide additional clear evidence for the independence of

834 space-based attentional control mechanisms in visual and tactile WM.

835   What do the observations of the present study imply for the architecture of

836 multimodal WM and its top-down control? The dynamic shifts of spatial attention

837 between WM representations and hemispheres that were observed in this and

838 previous sequential loading studies, as well as in experiments on multiple object

839 tracking (Drew et al. 2014a) could reflect the flexible updating of location pointers,

840 which control the activation profile of WM representations in modality-specific visual

841 or tactile spatial maps. The existence of such location pointers was initially proposed

842 as a mechanism for visual stability during saccadic eye movements (Cavanagh et al.

843 2010) and for the online tracking of visual objects (Oksama and Hyona 2008). The

844 Visual Indexing Theory (Pylyshyn 1989) proposes that objects are tracked via their

845 locations using spatial indices that convey no featural information about object-identity.

846 Similar pointer mechanisms could also be employed during the space-based

847 attentional control of WM maintenance. This hypothesis is compatible with accounts

848 proposing a map-based organization of WM (Franconeri, Alvarez, Cavanagh 2013),

849 where information is stored as hierarchical feature bundles (Brady, Konkle, Alvarez

850 2011) in distributed two-dimensional content maps. Objects in different sensory

851 modalites are stored in feature maps in modality-specific sensory areas, as suggested

852 by the sensory recruitment hypothesis of WM (Jonides, Lacey, Nee 2005). Because

853 maps in higher-level attentional control areas, such as prefrontal cortex, lack sensitivity

854 to low-level properties of stimuli (Serences 2016; Thompson and Bichot 2005), they

855 may instead provide the spatial pointer mechanisms that are necessary to select

856 particular items in WM in a top-down fashion. Such spatial indexing mechanisms for

857 individual memorized objects are particularly important if features of these objects

858   were represented in distributed modality-specific cortical maps. In this context, the

859   emergence of visual and tactile CDA component observed in the present study could

860   reflect the activation of WM representations in visual and tactile maps that is triggered

861   by top-down input from spatial pointers, and the polarity reversal of these components

862   on shift trials, the result of spatial updating processes within the location pointer

863   system. Our results suggest that spatial indexing occurs in parallel and independently

864   for objects stored in visual and tactile maps, allowing for strictly modality-specific

865   dynamic changes in the allocation of attention during WM maintenance.

866

867   **Conclusion:** Top-down control processes regulate the activation of representations

868   in sensory WM stores, and these processes operate in a dynamic and spatially

869   selective fashion. The maintenance of visual and tactile items is mediated by spatial

870   pointer mechanisms that specify the location of these items once they have been

871   encoded into WM. The independence of attention shifts within visual and tactile WM

872   indicates that the spatial indexing of somatotopic and retinotopic information is

873   mediated by parallel modality-specific processes that operate in distributed cortical

874   maps.

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Figure legends

Figure 1: Task design (A) In Experiment 1a, vision was the primary modality and touch was the secondary modality. Each visual sample set contained circles and squares on opposite sides. On stay trials (50%), the circles and squares in S2 were presented on the same side as in S1. On shift trials (50%), the shapes swapped their locations across S1 and S2. Participants memorized the colors of all target shapes (circles or squares, counterbalanced) in S1 and S2. In bimodal blocks, participants also memorized the locations of the tactile S1 stimuli on the same side as the visual S1 targets, as memory was unpredictably tested for vision or touch (50% match/mismatch). In unimodal blocks, memory was always tested for vision, and tactile stimuli could be ignored. (B) In Experiment 1b, touch was the primary modality. Tactile targets were defined by stimulus waveform (pulsed or continuous, counterbalanced). Participants memorized the locations of the S1 and S2 targets, either on the same hand or on different hands (50% stay/shift). In bimodal blocks, participants also memorized the colors of the visual S1 stimuli on the same side as the tactile S1 target, and memory was unpredictably tested for touch or vision. In unimodal blocks, only touch was tested. (C) In Experiment 2, bimodal S1 and S2 sample stimulus sets were followed unpredictably by a tactile or visual test set. Participants memorized the locations of visual targets defined by color (green/red) and tactile targets defined by waveform (pulsed/continuous). Visual and tactile S1 targets were always located on the same side, and the location of the S2 targets (same/different side) was orthogonally manipulated for touch and vision (50% stay or shift trials for each modality).

1026 **Figure 2. CDA components in Experiment 1a** CSDs recorded in unimodal and

1027 bimodal blocks contralateral and ipsilateral to the S1-targets (thick vs. thin lines) over

1028 brain regions associated with the primary task (vision: CDA, left panels) and secondary

1029 task (touch: tCDA, right panels) are shown separately for visual stay and shift trials.

1030 Visual CDA components changed polarity on shift trials in the period after S2, in both

1031 unimodal and bimodal blocks. Tactile CDA components were absent in unimodal

1032 blocks where touch was task-irrelevant but present in bimodal blocks. The tCDA

1033 remained present during the period following S2, and did not differ between visual stay

1034 and shift trials.

1035

1036 **Figure 3. Contra-/ ipsilateral difference waves from Experiment 1a and 1b (left**

1037 **vs. right column)** Visual and tactile CDA components associated with the primary

1038 modality (vision in Exp. 1a, touch in Exp. 1b) are shown in the two top panels for

1039 primary-modality stay and shift trials, separately for the unimodal and bimodal tasks.

1040 The panel below shows tactile and visual CDA components for the secondary modality

1041 in the bimodal task, separately for stay and shift trials in the primary modality. Note the

1042 different scales for the tCDA and CDA. Error bars/colored shadings indicate the

1043 confidence intervals for the true population mean. The topographical maps in the

1044 bottom panel display the distribution of lateralized delay activity during the S1- and S2-

1045 periods (top and bottom rows) for stay and shift trials in the unimodal and bimodal WM

1046 tasks of Experiments 1a and 1b.

1047

1048 **Figure 4. Behavioral performance in Experiments 1a, 1b and 2** (A) WM accuracy

1049 in Experiment 1a (top) and Experiment 1b (bottom), where vision or touch were the

1050 primary modalities, respectively. Visual and tactile WM performance on stay and shift

1051   trials is shown separately for the primary modality (in the unimodal and bimodal tasks)

1052   and for the secondary modality (in the bimodal task). (B) WM accuracy in Experiment

1053   2, for trials where memory was tested for the visual task (top) or tactile task (bottom),

1054   shown separately for stay and shift trials in the tested and untested modality.

1055

1056   **Figure 5. CSD amplitudes from Experiment 1b** CSDs measured over

1057   somatosensory and visual areas contralateral and ipsilateral to task-relevant side of

1058   S1 sample sets in the unimodal and bimodal tasks. The tCDA reversed polarity during

1059   the S2-period on tactile shift trials in both tasks. There was no corresponding polarity

1060   change of visual CDA components in the bimodal task on tactile shift trials.

1061

1062   **Figure 6. CSD amplitudes from Experiment 2** Visual and somatosensory CDA

1063   components recorded contra- and ipsilateral to task-relevant sample items in S1,

1064   shown separately for trials with a S1-S2 target location shift in neither modality, in

1065   vision only, touch only, or in both modalities. Visual and tactile CDA components

1066   reversed polarity in the S2-period on visual and tactile shift trials, respectively, but

1067   were unaffected by shifts in the other untracked modality. Note the different scales for

1068   visual and tactile CSDs.

1069

1070   **Figure 7. Contra-ipsilateral difference waves from Experiment 2.** The left panel

1071   shows visual CDA components elicited on visual stay and shift trials, separately for

1072   trials where the position of tactile targets in S1 and S2 remained the same or changed

1073   (Touch Stay versus Touch Shift, in green vs. red). The right panel shows the

1074   corresponding tactile tCDA components for tactile stay and shift trials (Vision Stay

1075   versus Vision Shift, in green vs. red). The line graphs show mean tCDA/CDA

1076 amplitudes in the S1 and S2 periods of all four trial conditions. Error bars/colored

1077 shadings indicate confidence intervals; note the different scales for the tCDA and CDA.

1078 Topographical maps show the distribution of lateralized delay activity during the S1-

1079 and S2-periods (top and bottom panels) for the four trial types.
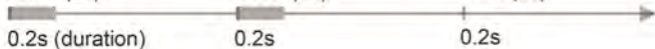
Event and timing (SOA)

Set 1 (0s)   Set 2 (1s)   Response period 1.8s
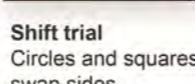   Test (2s)

0.2s (duration)   0.2s   0.2s

(A) Experiment 1a. Primary modality: Vision

Vision + Touch   Vision only   Vision or Touch

Shift trial
Circles and squares
swap sides

(B) Experiment 1b. Primary modality: Touch

Vision + Touch   Touch only   Vision or Touch

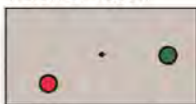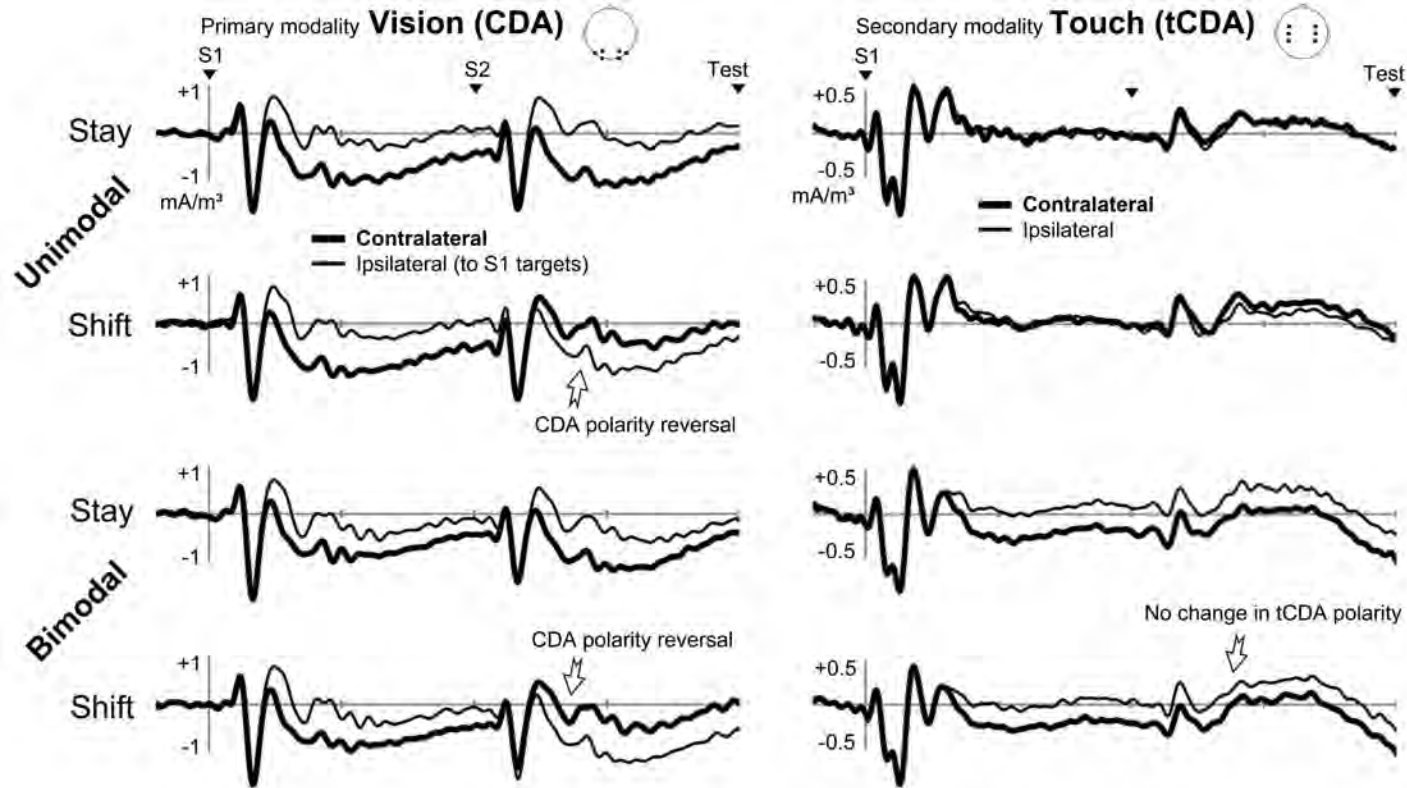**Shift trial** Pulsed
and continuous
waveforms swap
sides

Pulsed   Continuous

(C) Experiment 2

Vision + Touch   Vision + Touch   Vision or Touch
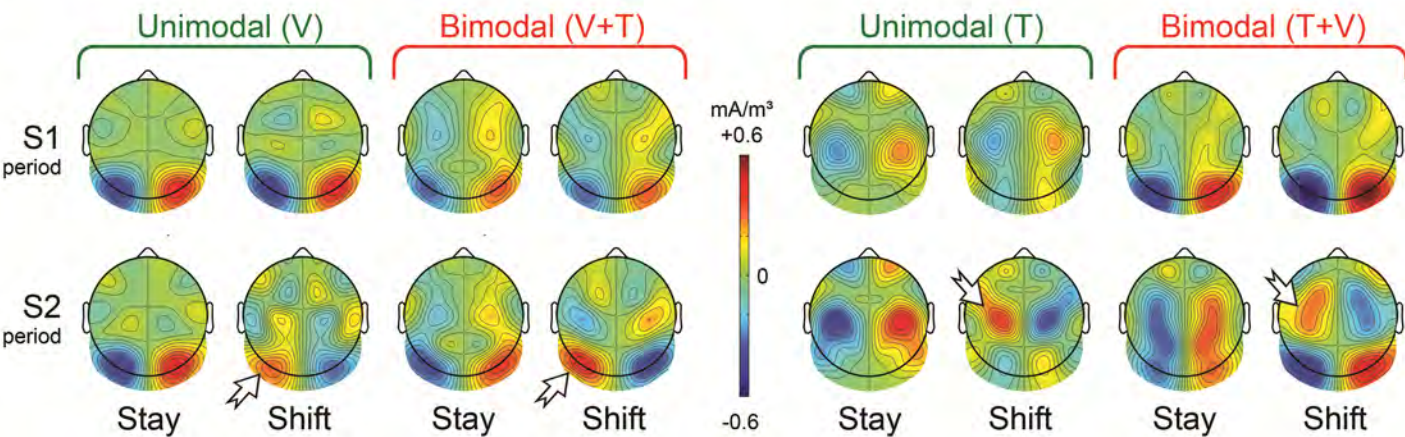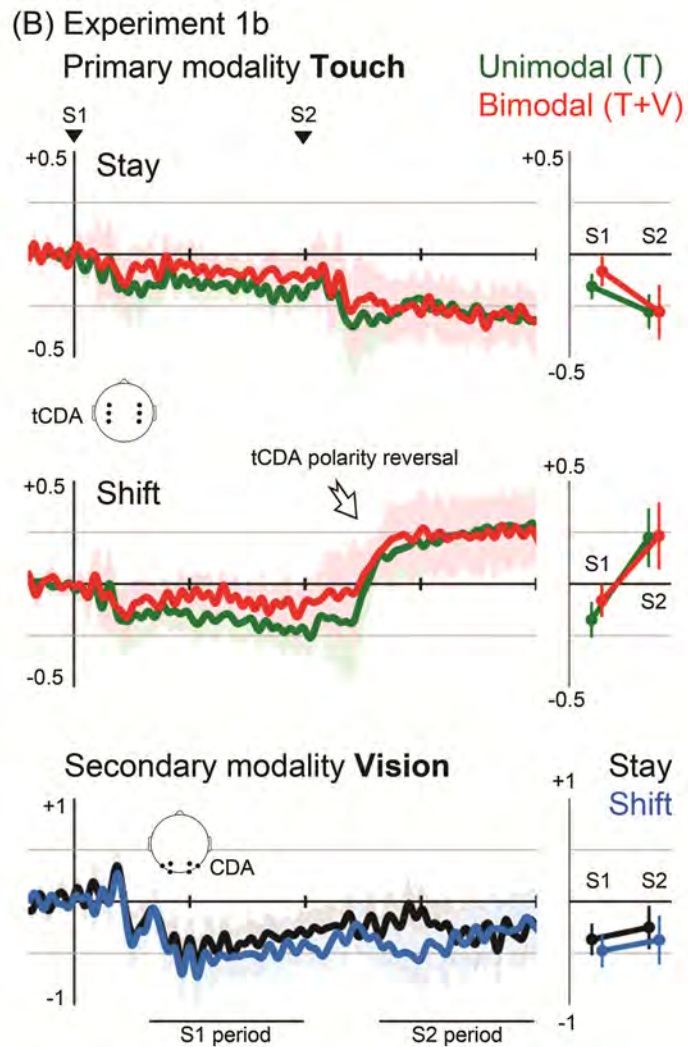
Primary modality Vision (CDA)

Unimodal

Stay — +1 / −1 mA/m³ — S1, S2, Test

Contralateral
Ipsilateral (to S1 targets)

Shift — +1 / −1 — CDA polarity reversal

Bimodal

Stay — +1 / −1

Shift — +1 / −1 — CDA polarity reversal

Secondary modality Touch (tCDA)

Stay — +0.5 / −0.5 mA/m³ — S1, Test

Contralateral
Ipsilateral

Shift — +0.5 / −0.5

Stay — +0.5 / −0.5

Shift — +0.5 / −0.5 — No change in tCDA polarity

(A) Experiment 1a
Primary modality **Vision**

Unimodal (V)
Bimodal (V+T)

Stay

CDA

CDA polarity reversal

Shift

Secondary modality **Touch**

tCDA

Stay
Shift

S1 period
S2 period

[mA/m³]

(B) Experiment 1b
Primary modality **Touch**

Unimodal (T)
Bimodal (T+V)

Stay

tCDA

tCDA polarity reversal

Shift

Secondary modality **Vision**

CDA

Stay
Shift

S1 period
S2 period

Unimodal (V)   Bimodal (V+T)

S1 period

S2 period

Stay   Shift   Stay   Shift

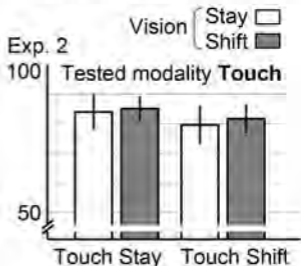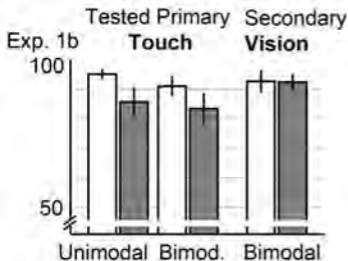mA/m³
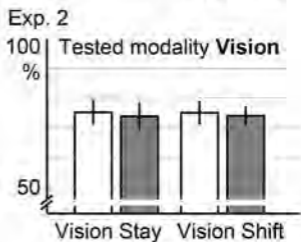+0.6

0

−0.6

Unimodal (T)   Bimodal (T+V)

S1 period

S2 period

Stay   Shift   Stay   Shift

(A) Primary modality [Stay □ / Shift ■]

Exp. 1a — Tested Primary **Vision**, Secondary **Touch**

Exp. 1b — Tested Primary **Touch**, Secondary **Vision**

(B) Touch [Stay □ / Shift ■]

Exp. 2 — Tested modality **Vision**

Vision [Stay □ / Shift ■]

Exp. 2 — Tested modality **Touch**

Primary modality **Touch (tCDA)** | Secondary modality **Vision (CDA)**

S1 | S2 | Test | S1 | Test

Unimodal

Stay
+0.5
−0.5
mA/m³

+1
−1
mA/m³

— **Contralateral**
— Ipsilateral (to S1 targets)

— **Contralateral**
— Ipsilateral

Shift
+0.5
−0.5

+1
−1

tCDA polarity reversal

Bimodal

Stay
+0.5
−0.5

+1
−1

Shift
+0.5
−0.5

+1
−1

tCDA polarity reversal

No change in CDA polarity

Vision (CDA)

Shift None
+1
-1
mA/m³

Contralateral
Ipsilateral (to S1 targets)

Shift Vision
+1
-1
CDA polarity reversal

Shift Touch
+1
-1

Shift Both
+1
-1
CDA polarity reversal

Touch (tCDA)

Shift None
+0.5
-0.5
mA/m³

Contralateral
Ipsilateral

Shift Vision
+0.5
-0.5

Shift Touch
+0.5
-0.5
tCDA polarity reversal

Shift Both
+0.5
-0.5
tCDA polarity reversal

S1 · S2 · Test