

ORIGINAL ARTICLE

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.

Key words: Electroencephalography (EEG), event-related potentials (ERPs), Multisensory (tactile/visual), Spatial attention, Working memory (WM)

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 processes. Several lines of evidence point toward a critical role of spatial attention during the encoding and storage of sensory signals in WM (Awh et al. 2006). WM maintenance relies on frontoparietal networks that are also involved in the control of

spatial attention (Awh and Jonides 2001). The sustained activity of neurons in prefrontal cortex that is observed during the delay period of WM tasks is selectively tuned to memorized object locations on the contralateral side (Funahashi 2013). The role of spatial attention for feature binding and the formation of object-based representations in WM has been demonstrated by space-based competition effects (Robertson 2003). For example, decreasing the spatial distance between competing stimuli reduces WM precision and increases binding errors in WM (Emrich and Ferber 2012; Ahmad et al. 2017).

Electrophysiological studies of WM have provided additional evidence for links between WM maintenance and space-based attentional control processes. Spatial location appears to be represented in an obligatory fashion in visual WM, even when it is task-irrelevant (Kuo et al. 2009; Katus et al. 2012; Foster et al. 2017). The maintenance of sensory signals in WM during the delay periods of lateralized visual and tactile change detection tasks is associated with spatially selective modulations of event-related potentials (ERPs). Visual WM maintenance gives rise to a sustained negativity contralateral to the to-be-memorized visual objects (Vogel and Machizawa 2004), and an analogous contralateral negativity has also been found in tactile WM tasks (Katus et al. 2015a). This visual contralateral delay activity (CDA) and its tactile equivalent (tCDA component) have modality-specific topographies over visual and somatosensory cortex, respectively. They reflect spatially selective modulations of neural activity in modality-specific sensory-perceptual cortical areas, in line with the sensory recruitment account of WM (Postle 2006). The fact that CDA and tCDA amplitudes both increase with the number of visual or tactile stimuli that have to be maintained, and the fact that both are sensitive to individual differences in WM capacity (Vogel and Machizawa 2004; Katus et al. 2015a) demonstrate that these 2 components are linked to WM maintenance processes in vision and touch.

Evidence that CDA components do not reflect the generic storage of content in WM, but more specifically the attentional activation of WM representations comes from studies that used retro-cue and sequential loading procedures (see also McElree, 2001; Oberauer and Hein, 2012 for discussions of links between attention and WM storage). In retro-cue experiments, observers initially encode stimuli on both sides, before a cue indicates the task-relevant items for the current trial. Retro-cues trigger shifts of attention toward representations that are already stored in WM. These attention shifts were found to modulate the CDA and tCDA components in visual (Eimer and Kiss 2010) and tactile (Katus et al. 2015b) retro-cue experiments. In sequential loading tasks, participants memorize task-relevant target stimuli in 2 sequentially presented sample sets (S1, S2). When the target items in S1 and S2 are presented on opposite sides, CDA components are initially triggered contralateral to the S1 targets, but then reverse polarity during the S2 period, reflecting the task-relevant item locations in the second sample set. This polarity reversal was observed for the tCDA in a tactile WM experiment (Katus and Eimer 2015) and for the CDA during the sequential loading of visual WM (Berggren and Eimer 2016), indicating shifts of spatial attention toward the contralateral side of somatotopic or retinotopic space during the S2 period (see also Drew et al., 2014b for an analogous polarity reversal of visual CDA components during continuous object tracking when visual 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 electroencephalography (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 et al. 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. Sauls and Cowan 2007; Fougner and Marois 2011; Cowan et al. 2014), suggesting that some aspect of WM processing in a given modality is impaired when items in another modality have to be simultaneously maintained. If these bimodal costs were associated with the need to coordinate shared spatially selective attentional control processes across sensory modalities, they should be particularly pronounced under conditions where to-be-memorized items in different modalities are presented at spatially incongruent locations. Such spatial congruency effects on multimodal WM performance have not yet been investigated systematically. One exception is a recent ERP study from our lab (Katus and Eimer 2016) where participants memorized 2 tactile and 2 visual sample stimuli that were either presented on the same side or on opposite sides. In same-side blocks, visual and tactile CDA components were elicited over the same hemisphere, each with their typical modality-specific topography. In opposite-side blocks, these components emerged over different hemispheres, contralateral to the respective task-relevant visual and tactile sample items. Critically, visual and tactile CDAs were elicited at the same time and were identical in amplitude in same-side and opposite-side blocks, and WM performance did not differ between these 2 types of blocks. The absence of any behavioral or electrophysiological evidence for impaired visual and tactile WM maintenance processes in the opposite-side blocks of this experiment suggests that these processes are controlled by parallel and entirely independent modality-specific mechanism of spatial attention.

The apparent independence of space-based attentional control processes during visual and tactile WM maintenance suggested by the results of this previous EEG experiment (Katus and Eimer 2016) contrasts with previous evidence for crossmodal synergies in spatial attention (Spence and Driver 1996; Eimer and van Velzen 2002; Eimer et al. 2002), and is also inconsistent with claims that WM storage in multisensory tasks is based on shared central control mechanisms (Cowan 2011). It is possible that these results are specific to the particular task conditions that were realized in this experiment. The fact that the side of task-relevant visual and tactile sample items was specified in advance and remained constant for an entire block enabled participants to activate constant attentional task sets for the relevant visual and tactile locations prior to the start of each block. Furthermore, because all sample stimuli were presented

simultaneously, no dynamic re-allocations of spatial attention between WM representations were required in this experiment. These 2 factors may have been responsible for the absence of any evidence of impaired WM maintenance in the opposite-side blocks of our previous CDA study (Katus and Eimer 2016). Spatial synergies in the attentional control of WM maintenance in bimodal tasks may emerge primarily under conditions where the locations of task-relevant memory sample items vary unpredictably across trials, and where attention has to shift rapidly between WM representations within and across sensory modalities. This was tested in the present study.

We employed sequential loading procedures in bimodal visual/tactile WM tasks. At the start of each trial, bimodal sample sets (S1) were presented, which were followed after a delay period by a second sample set (S2), and then, after another delay period, by a memory test display (vision or touch). The identity of the to-be-memorized visual sample items was indicated by their shape (Experiment 1) or color (Experiment 2), and task-relevant tactile items were defined by stimulus waveform (pulsed vs. continuous; in Experiments 1b and 2). These relevant visual and tactile items (targets) were always accompanied by task-irrelevant items on the opposite side of the sample sets. The critical manipulation concerned the need to shift attention in either touch or vision in the period following S2. Tactile or visual S2 target items were presented either on the same side or on the opposite side as the S1 targets in the same modality. To track the activation of visual and tactile WM representations, we measured CDA and tCDA components during the periods following S1 and S2.

In Experiment 1, the sequential loading task was performed for one primary modality (vision in Experiment 1a, touch in Experiment 1b) and a secondary modality (touch or vision in Experiments 1a and 1b, respectively). S1 always contained items in both modalities, and task-relevant visual and tactile items were always presented on the same side. S2 only contained primary-modality items, and the to-be-memorized targets appeared unpredictably either on the same side as the target items in S1 or on the opposite side (stay/shift trials; see Fig. 1). Participants were instructed to memorize the primary-modality target items in S1 and S2, while also maintaining the secondary-modality S1 targets across both delay periods. Memory was unpredictably tested for either modality. For vision, participants reported the presence/absence of a color change between task-relevant visual sample and test stimuli. For touch, the presence/absence of a location change had to be reported. In addition to these bimodal task blocks, there were also unimodal baseline blocks where stimulus presentation procedures were identical but WM was always tested for the primary modality, so that S1 items for the secondary modality could be entirely ignored.

In unimodal blocks, reliable CDA components should only be elicited in the currently task-relevant primary modality, but should not be present over sensory areas for the secondary irrelevant modality. Visual and tactile CDA components for the primary modality were expected to change polarity on switch trials but not on stay trials, reflecting the dynamic re-allocation of spatial attention in response to S2 (Katus and Eimer 2015; Berggren and Eimer 2016). If WM maintenance in vision and touch 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.

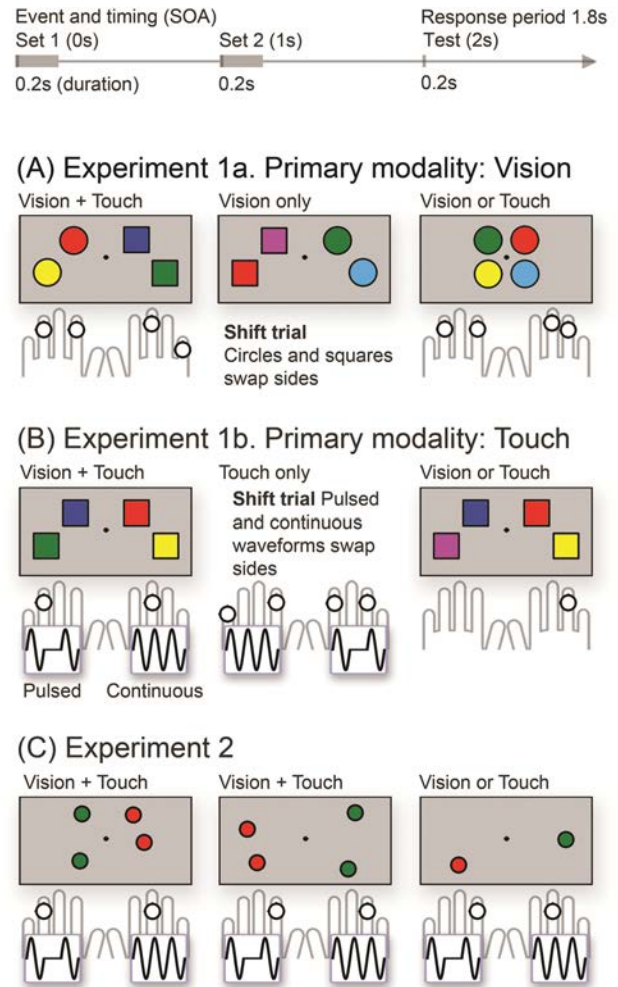


Figure 1. Task design (A) In Experiment 1a, vision was the primary modality and touch was the secondary modality. Each visual sample set contained circles and squares on opposite sides. On stay trials (50%), the circles and squares in S2 were presented on the same side as in S1. On shift trials (50%), 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).

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 vs. opposite side as in S1) was varied randomly and orthogonally, resulting in 4 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. Forty-nine paid volunteers participated in the 3 experiments. Five 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, 30 years mean age, 7 female, 10 right-handed; Experiment 1b: 16 participants, 29 years mean age, 11 female, 13 right-handed; Experiment 2: 16 participants, 30 years 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 × 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 8 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 8-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).

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 3 sets were separated by intervals of 1000 ms. Each visual sample set included 2 squares on one monitor side and 2 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 Fig. 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 4 task-relevant target shapes in the S1 and S2 displays, 4 out of 6 possible colors were selected on each trial (Commission Internationale de l'Eclairage [CIE] color coordinates: red = 0.627/0.336; green = 0.263/0.568; blue = 0.189/0.193; yellow = 0.422/0.468; cyan = 0.212/0.350; magenta = 0.289/0.168). The 4 colors of the 4 task-irrelevant shapes in these displays were selected independently from this set of 6 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 locations, so that 4 colors at 4 different locations had to be memorized after S2; see Fig. 1. Visual test sets involved 4 target shapes in a 2-by-2 matrix at central fixation (0.46 ° horizontal and vertical eccentricity). On visual match trials (50%), the 4 memorized target colors were repeated. Their spatial arrangement (top/bottom, left/right) matched the location of the memorized colors in the S1 and S2 displays. On visual mismatch trials (50%), the color 1 of the 4 test display items was replaced by a different not-memorized color.

Four identical tactile sample stimuli (100 Hz vibrations, intensity: 0.37 N) were presented to 2 randomly selected fingers on the left and right hand, simultaneously with the visual S1 displays. In bimodal blocks, participants were instructed to memorize the locations of the tactile samples on the same side where the task-relevant visual S1 sample shapes were presented. On half of all trials, pairs of tactile stimuli were presented to the left and right hand at memory test. On tactile match trials (50%), the 2 tactile test items on the task-relevant hand appeared at the same locations as in S1. On tactile mismatch trials (50%), 1 of these 2 stimuli appeared at a different location. The tactile locations on the other task-irrelevant hand were selected in the same way for each tactile test set (50% match and mismatch trials for S1 items presented to the irrelevant hand). Matches and mismatches on the attended and unattended hands were uncorrelated. In unimodal blocks, only visual memory test displays were presented, and participants could therefore ignore the tactile stimuli that appeared concurrently with visual S1 displays. Experiment 1a included 12 blocks with 48 trials per block (576 trials in total, 144 trials for each of the 4 combinations of stay/shift trials and unimodal/bimodal blocks). The unimodal and bimodal WM tasks were performed in 6 successive blocks, with task order counterbalanced across participants.

Experiment 1b

Touch was the primary modality, vision was the secondary modality. Tactile targets were defined by stimulus waveform (counterbalanced across participants, continuous: 200 ms vibration, or pulsed: 2 10 ms pulses followed by 2 10 ms pulses after a 160 ms gap). Two tactile sample sets (S1 and S2) were presented on each trial. S1 included 2 tactile stimuli (one continuous, one pulsed), each delivered to a randomly selected finger of each hand. At S2, 2 different fingers of each hand were stimulated. One hand received a pair of pulsed stimuli, the other a pair of continuous stimuli). In stay trials, all continuous and all pulsed tactile S1 and S2 stimuli were presented to the same hand. In shift trials, continuous and pulsed stimuli swapped sides between S1 and S2, so that the to-be-memorized tactile stimuli were presented to opposite hands. Bilateral visual sample stimuli (identical to Experiment 1a) were presented simultaneously with the tactile S1 sets. No visual samples appeared at S2. In bimodal blocks, participants memorized all tactile S1 and S2 targets, as well as the visual S1 stimuli that were located on the same side as the tactile S1 targets. Memory was unpredictably tested for touch or vision. Visual memory test sets were identical to the sample sets, except that on mismatch trials (50%), one of the sample colors on the task-relevant side was replaced by a different color. Tactile memory test sets included one continuous and one pulsed stimulus, delivered to different hands. Participants had to decide whether the location of the task-relevant (continuous or pulsed) tactile test stimulus matched the location of one of the 3 task-relevant tactile sample stimuli (match trials, 50%) or was presented at a different location (mismatch trials, 50%). In unimodal blocks, only touch was tested, and visual S1 stimuli could be ignored.

Experiment 1b included 12 blocks with 48 trials per block (576 trials in total, 144 trials for each of the 4 combinations of stay/shift trials and unimodal/bimodal blocks). The unimodal and bimodal WM tasks were performed in 6 successive blocks, counterbalanced across participants. Two procedural changes relative to Experiment 1a were introduced for pragmatic reasons. First, participants memorized 2 visual targets at S1 and S2, while in Experiment 1b, they had to memorize 1 tactile S1 and 2 tactile S2 targets. This was necessitated by the fact that there were only 4 tactile stimulus locations for each hand, and that a tactile WM load of 2 items for S1 and S2 would have resulted in all 4 fingers of the same hand receiving a target stimulus on stay trials. Second, the locations of visual S1 targets varied unpredictably across trials in Experiment 1a, whereas the location of tactile S1 targets (and thus the location of visual targets in bimodal blocks) remained constant in each block in Experiment 1b, and was changed every 3 blocks (with the task-relevant side for the first block having been randomly determined per participant). This was done because pilot data indicated that a trial-wise randomization of tactile S1 target locations would have resulted in an extremely challenging task. Critically for the purposes of the present study, the location of tactile S2 targets (same vs. opposite side) remained entirely unpredictable.

Experiment 2

Participants concurrently performed sequential loading tasks in both modalities, with bimodal S1 and S2 sets followed unpredictably by a unimodal tactile or visual test set. As in Experiment 1b, the task-relevant tactile and visual S1 targets were located on the same side (left or right), and this location remained constant within each block, and was changed every 3 blocks. Critically, the

locations of the task-relevant visual and tactile sample stimuli in S2 were orthogonally randomized for each modality (stay vs. shift, 50%), resulting in the need to shift attention in the period after S2 in neither modality (25%), in only one modality (touch or vision, 25% each), or in both modalities simultaneously (25%). In contrast to Experiment 1, where participants had to retain the colors of visual samples and the locations of tactile samples, they memorized stimulus locations for both modalities in Experiment 2. This change was introduced because a common representational format for stimuli in different modalities has been reported to produce crossmodal interference in previous auditory-visual WM tasks (see Exp. 8 in Fougnet et al. 2015).

Each visual sample set included pairs of 2 green and 2 red circles (stimulus size: 0.40° of visual angle) on opposite sides. These stimuli were presented on 2 virtual (invisible) concentric rings around the fixation dot (radius relative to fixation: 1.86° and 1.29° for the outer and inner rings). All 4 stimuli in each sample display appeared at the same eccentricity. On trials where S1 items were located in the inner ring, S2 items were located on the outer ring, or vice versa; see Fig. 1. Stimulus locations were randomly sampled from 140 angular positions (in polar coordinates: 110° to 250° for the left side, 290° to 70° for the right side) with the constraint that the stimulus pairs on each side of the sample displays were separated by a minimum distance of 80° . To-be-memorized visual target stimuli were defined by their color (green or red, counterbalanced across participants). Participants now had to memorize the locations of the task-relevant visual sample stimuli in S1 and S2. Visual memory test displays contained one green and one red circle on opposite sides. Participants had to decide whether the location of the target-color test item matched the location of one of the visual target items in S1 and S2. This was the case in half of all trials where visual WM was tested. In the remaining 50% mismatch trials, the target-color item in the test display appeared at a different location, at an angular distance of 40° relative to one of the memorized locations in S1 or S2.

Tactile sample and test stimuli were identical to those used in Experiment 1b (tactile targets: continuous or pulsed, counterbalanced across participants), with the exception that only a single task-relevant tactile item was presented both at S1 and S2. Each tactile sample set included a target and a distractor stimulus, presented to opposite hands. S2 samples were never presented to any location stimulated at S1. The task-relevant tactile stimulus in the test set either matched the location of one of the 2 tactile targets in S1 or S2, or was presented to a non-target location (50% match/mismatch). Experiment 2 included 16 blocks with 34 trials per block (544 trials in total; 136 trials for each of the 4 combinations of tactile stay/shift and visual stay/shift trials). The task-relevant side for S1 was randomly determined for block 1, and changed to the opposite side in block 9.

Analysis of EEG Data

Acquisition and Pre-processing

EEG data, sampled at 500 Hz using a BrainVision direct current (DC) amplifier, were 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 horizontal eye movements (horizontal electrooculogram, HEOG). Continuous EEG data were referenced to the left mastoid during recording, and re-referenced to the arithmetic mean of both

mastoids for data pre-processing. Data were offline low-pass filtered (20 Hz, Blackman window, filter order 1000). All EEG results reported below were virtually identical when a higher low-pass cut-off of 40 Hz was employed. Epochs were extracted for the 2 s period after the sample set, and were corrected relative to a 200 ms pre-stimulus baseline.

Artifact Rejection and Correction

We first rejected trials with saccades using a differential step function that ran on the bipolarized HEOG (step width 100 ms, threshold 30 μ V) prior to artifact correction. 'Independent component analysis' (Delorme et al. 2007) was employed to correct for frontal artifacts such as eye blinks, and residual traces of horizontal eye movements that had not been detected by the step function. We further rejected trials in which difference values for corresponding left- minus right-hemispheric electrodes, averaged between 300 and 2000 ms after S1, exceeded a fixed threshold of ± 80 μ V (for any electrode pair), as well as trials where difference values exceeded ± 4 standard deviations per individual dataset (for at least 2 electrode pairs). The remaining EEG epochs entered 'Fully automated statistical thresholding for EEG artifact rejection' (Nolan et al. 2010) for the interpolation of noisy electrodes, and were subsequently converted to current source densities (CSDs: iterations = 50, $m = 4$, $\lambda = 10^{-5}$; Tenke and Kayser 2012). A total of 93.4% of all epochs were retained for analysis after artifact rejection (Experiment 1a: 92.9%, Experiment 1b: 93.2%, Experiment 2: 93.8%). Statistical tests were based on correct and incorrect trials, since the

exclusion of incorrect trials did not change the pattern of results, but would have reduced the signal-to-noise ratio of EEG data.

Electrodes and EEG Analyses

CSDs were separately averaged across 3 adjacent electrode pairs contralateral and ipsilateral to the task-relevant side. Tactile CDA (tCDA component) was measured at lateral central scalp regions (C3/4, FC3/4, CP3/4), and visual CDA was measured at lateral occipital regions (PO7/8, PO3/4, O1/2). The electrode locations used to quantify tCDA and CDA components were identical to those employed in previous studies (Katus and Eimer 2016; Katus et al. 2017; Katus and Eimer 2018a, 2018b). Separate CDA/tCDA components were computed for the delay periods following the 2 sample sets (S1 and S2), based on averaged CSDs obtained between 300 and 1000 ms following the onset of S1 or S2 (e.g., Vogel and Machizawa 2004; Katus and Eimer 2015). Statistical tests of neural activity during these periods were conducted on difference values of contra-minus ipsilateral CSDs. Error bars in graphs indicate 95% confidence intervals (CIs) for the true population mean. Thus, error bars that do not overlap with the zero axis ($y \neq 0$) indicate statistical significance of tCDA/CDA components; error bars that do not overlap with chance level ($y \neq 50\%$) indicate behavioral performance that is significantly above chance.

Spline-interpolated topographical voltage maps were computed as follows. First, we averaged CSD amplitudes for the time windows of interest. These data were collapsed across trials with left and right S1 targets by flipping electrode coordinates over the midline for trials with left-side S1 targets. Trials were

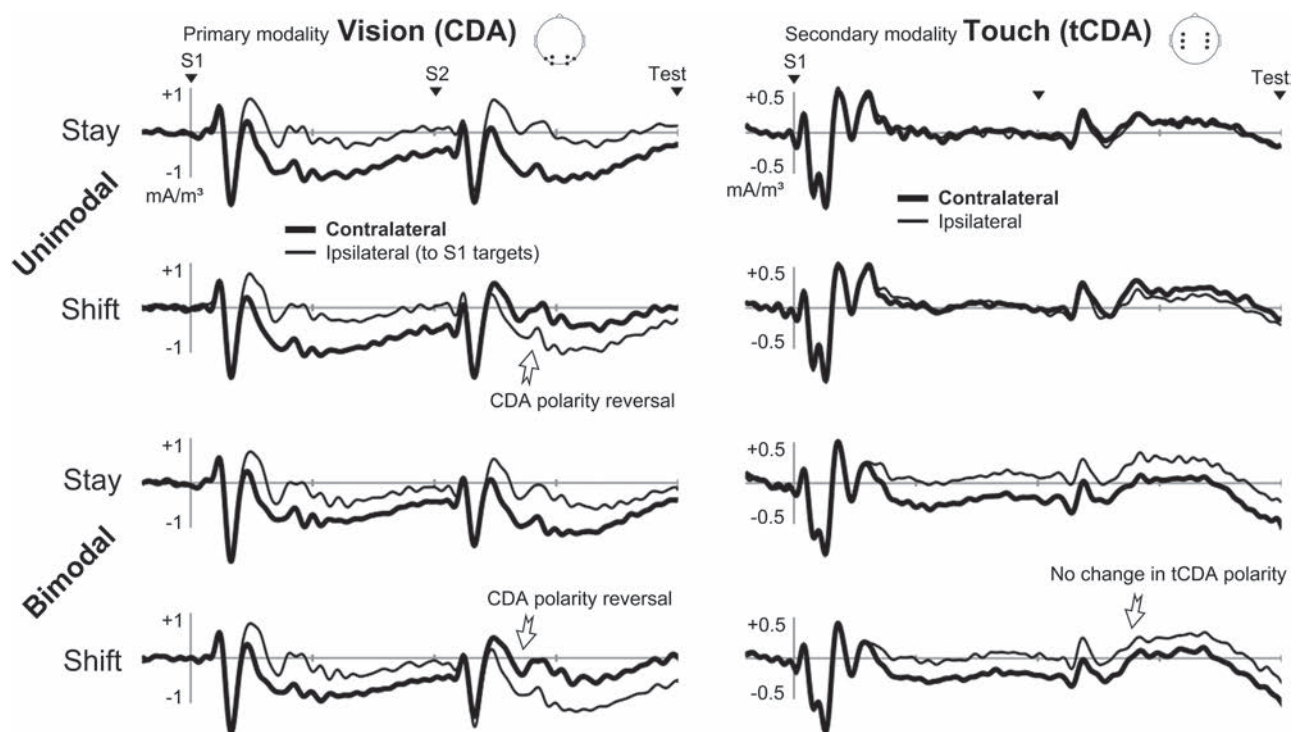


Figure 2. CDA components in Experiment 1a CSDs recorded in unimodal and bimodal blocks contralateral and ipsilateral to the S1 targets (thick vs. thin lines) over brain regions associated with the primary task (vision: CDA, left panels) and secondary task (touch: tCDA, right panels) are shown separately for visual stay and shift trials. Visual CDA components changed polarity on shift trials in the period after S2, in both unimodal and bimodal blocks. Tactile CDA components were absent in unimodal blocks where touch was task-irrelevant but present in bimodal blocks. The tCDA remained present during the period following S2, and did not differ between visual stay and shift trials.

then averaged separately for each experimental condition. To calculate contra-/ipsilateral difference values, we used a copy of the data, and after flipping electrode coordinates over the midline, we subtracted this inverted copy from the original data. This procedure eliminates any non-lateralized activity, thereby revealing lateralized effects that reflect amplitude differences between corresponding left- versus right-hemisphere electrodes. Note that the resulting full topographical maps are essentially equivalent to maps where the inverse of the contra-/ipsilateral amplitude difference measured over one hemisphere is projected to the other hemisphere. As a result, these full topographic maps show a symmetrical distribution of lateralized activity, which enhances the visibility of tCDA and CDA components, and highlights the fact that the polarity of these components can vary independently. In these maps, tCDA/CDA components evoked by the S1 targets appear as negativity over the left hemisphere, and tCDA/CDA polarity reversals during the period following S2 as a positivity over the left hemisphere (i.e., a negativity over the right hemisphere).

Bayes Factor Analysis

Conventional null-hypothesis significance tests can provide evidence against the null hypothesis, but cannot confirm the null hypothesis for a particular effect or interaction. We calculated Bayes factors using Bayesian t-tests (Rouder et al. 2009) and the software Jasp (JASP team 2016) to formally decide between the alternative and null hypotheses (i.e., presence vs. absence of a modulation) for each main effect/interaction in our statistical designs. The Bayes factor for the null-hypothesis (BF_{01}) corresponds to the inverse of the Bayes factor for the alternative hypothesis (BF_{10}), and indexes the relative evidence in the data for the absence rather than presence of a statistical difference. We always report the numerically larger BF. Reliable evidence for either hypothesis is marked by a $BF > 3$ (Jeffreys 1961), suggesting that the empirical data are at least 3 times more likely under this hypothesis as compared to the competing hypothesis.

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 Fig. 3A. As illustrated in the left panels of Fig. 2, the maintenance of visual sample stimuli in WM elicited visual CDA components in all experimental conditions. Note: 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, and the reliable presence of these components is shown in Figs 3 and 7, where statistically reliable modulations are indicated by error bars that do not overlap with the zero-axis (see Materials and Methods for further details). 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 Fig. 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; Fig. 3A.

Primary Modality (Vision, CDA Components)

CSD values obtained during the delay period following S2 were analyzed by separate ANOVAs with the factors 'Task type' (unimodal vs. bimodal) and 'Trial type' (stay vs. shift). Because stay versus shift trials only differed with respect to the side where visual S2 targets were presented, these trials were collapsed for the analysis of CDAs during the S1 period. CDA amplitudes were reduced in the bimodal task where both tactile and visual S1 targets had to be maintained relative to the unimodal task where touch was irrelevant. These bimodal costs for CDA amplitudes were present both during the S1 period ('Task type': $t(11) = 3.900$, $P = 0.003$, $BF_{10} = 18.689$) and during the S2 period ('Task type': $F(1,11) = 9.859$, $P = 0.009$, $BF_{10} = 6.217$). CDA components reversed polarity during the S2 period on shift trials but not on stay trials ('Trial type': $F(1,11) = 35.986$, $P = 10^{-4}$, $BF_{10} = 317.813$). Importantly, the size of this CDA difference between stay and shift trials was identical in unimodal and bimodal blocks ('Task type' $\times$ 'Trial type': $F(1,11) = 0.067$, $P = 0.800$, $BF_{01} = 3.379$); see Fig. 3, left side.

A follow-up ANOVA tested whether the reduction of CDA amplitudes in bimodal as compared to unimodal blocks, which was already present in the S1-period, might have obscured any interaction between 'Task type' and 'Trial type' in the S2 period. To eliminate any effects associated with CDA amplitude differences during the first delay period, we used the full S1 period as a new baseline, by subtracting CDA amplitudes measured in the S1 period from those measured after S2. This subtraction eliminated the 'Task type' main effect ($F(1,11) = 0.070$, $P = 0.796$, $BF_{01} = 3.375$) and increased the 'Trial type' effect ($F(1,11) = 48.031$, $P < 10^{-4}$, $BF_{10} = 970.181$) for CDAs during the S2 period. Critically, there was still no interaction between these 2 factors ('Task type' $\times$ 'Trial type': $F(1,11) = 0.009$, $P = 0.926$, $BF_{01} = 3.466$). These results demonstrate that the sustained maintenance of tactile information on one side in bimodal blocks had no effect on the polarity shift of visual CDA components on switch versus stay trials.

Secondary Modality (Touch, tCDA Component)

The tCDA was analyzed in the same fashion as the CDA (see above). A reliable tCDA component was elicited during the S1 period in the bimodal task ($t(11) = 5.590$, $P < 10^{-3}$, $BF_{10} = 189.203$), but not in the unimodal task ($t(11) = 0.656$, $P = 0.526$, $BF_{01} = 2.894$; main effect of 'Task type': $t(11) = 5.114$, $P < 10^{-3}$, $BF_{10} = 101.232$). This tCDA difference between the bimodal and unimodal tasks persisted during the S2 period ('Task type': $F(1,11) = 12.237$, $P = 0.005$, $BF_{10} = 10.456$). There were no other significant effects in the S2 period ('Trial type': $F(1,11) = 1.816$, $P = 0.205$, $BF_{01} = 1.670$; 'Trial type' $\times$ 'Task type': $F(1,11) = 0.336$, $P = 0.574$, $BF_{01} = 3.012$). In bimodal blocks, tCDA amplitudes during the S2 period did not significantly differ between visual stay and shift trials ($t(11) = 0.602$, $P = 0.560$, $BF_{01} = 2.978$). This result did not change after subtracting an S1-period baseline from tCDA amplitudes in the S2-period ($t(11) = 0.163$, $P = 0.874$, $BF_{01} = 3.440$), indicating that attention shifts in the primary visual modality did not affect concurrent tactile WM maintenance processes.

Behavioral Data

Participants responded correctly in 85.1% of trials when memory was tested for the primary modality (vision). The

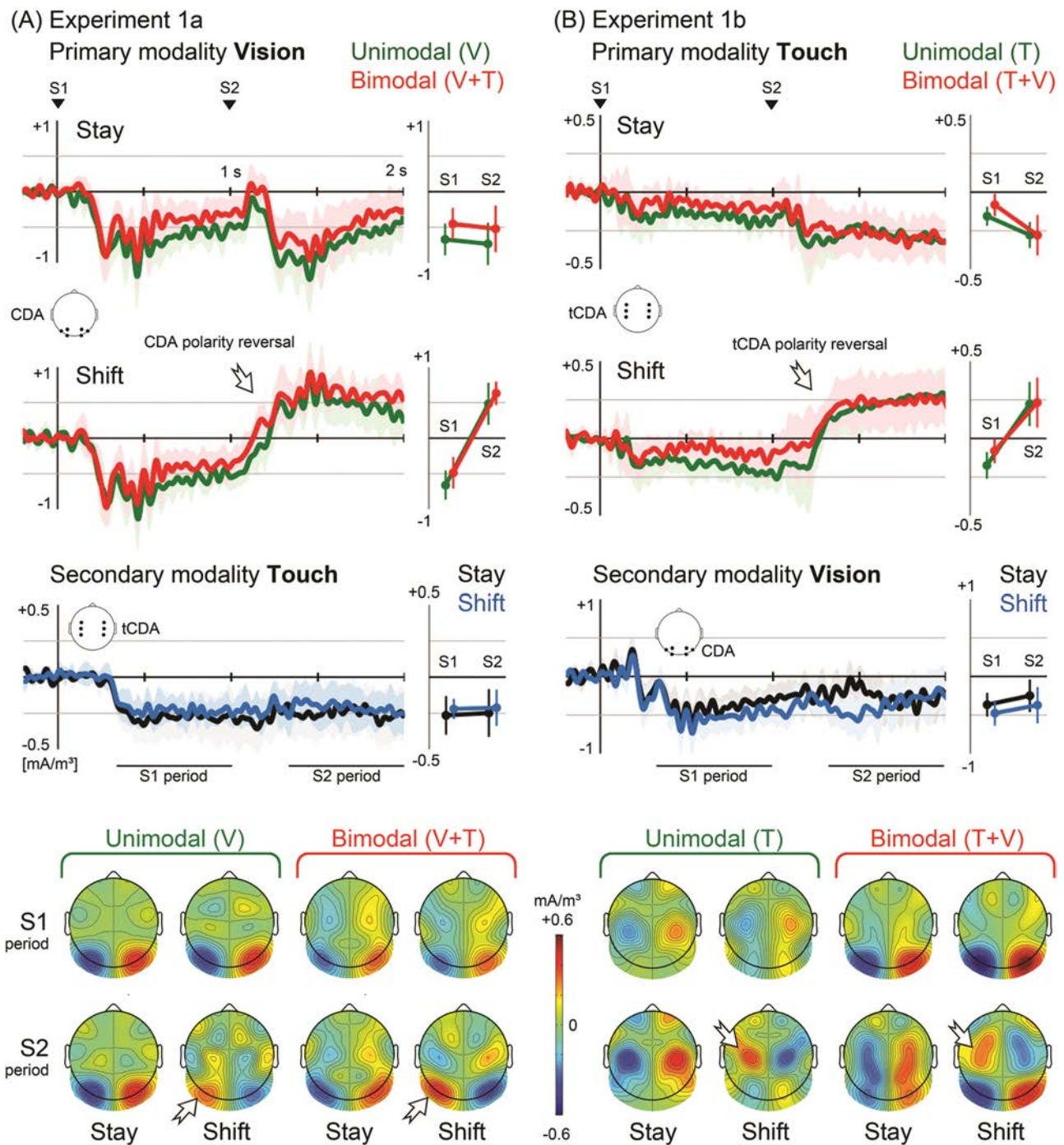


Figure 3. Contra-/ipsilateral difference waves from Experiment 1a and 1b (left vs. right column). Visual and tactile CDA components associated with the primary modality (vision in Experiment 1a, touch in Experiment 1b) are shown in the 2 top panels for primary-modality stay and shift trials, separately for the unimodal and bimodal tasks. The panel below shows tactile and visual CDA components for the secondary modality in the bimodal task, separately for stay and shift trials in the primary modality. Note the different scales for the tCDA and CDA. Error bars/shadings indicate the CIs for the true population mean. The topographical maps in the bottom panel display the distribution of lateralized delay activity during the S1 and S2 periods (top and bottom rows) for stay and shift trials in the unimodal and bimodal WM tasks of Experiments 1a and 1b.

accuracy on trials in the bimodal WM task where memory was tested for touch was 87.9%. Accuracy for the visual WM task was reduced in bimodal relative to unimodal blocks (83.2% vs. 87.0% correct; ‘Task type’: $F(1, 11) = 18.076$, $P = 0.001$, $BF_{10} = 30.861$); see Fig. 4A. There were no other significant effects or interactions for visual WM performance (‘Trial

type’ $\times$ ‘Task type’: $F(1, 11) = 0.311$, $P = 0.588$, $BF_{01} = 3.044$; ‘Trial type’: $F(1, 11) = 0.991$, $P = 0.341$, $BF_{01} = 2.299$). Accuracy for the tactile WM task in bimodal blocks was not significantly reduced in visual shift as compared to stay trials (86.4% vs. 89.4% correct; ‘Trial type’: $t(11) = 1.979$, $P = 0.073$, $BF_{10} = 1.242$).

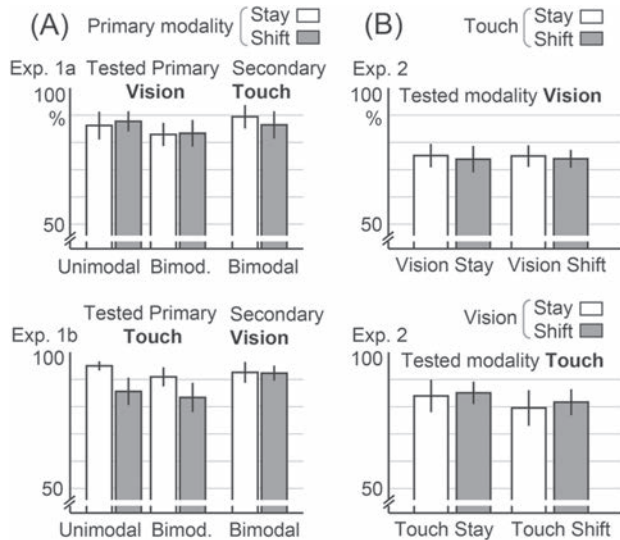


Figure 4. Behavioral performance in Experiments 1a, 1b, and 2. (A) WM accuracy in Experiment 1a (top) and Experiment 1b (bottom), where vision or touch were the primary modalities, respectively. Visual and tactile WM performance on stay and shift trials is shown separately for the primary modality (in the unimodal and bimodal tasks) and for the secondary modality (in the bimodal task). (B) WM accuracy in Experiment 2, for trials where memory was tested for the visual task (top) or tactile task (bottom), shown separately for stay and shift trials in the tested and untested modality.

Experiment 1b

In Experiment 1b, touch was the primary and vision secondary modality. Tactile and visual CDA components elicited by tactile and visual sample stimuli are shown in Fig. 5, and the corresponding difference waveforms are displayed in Fig. 3B. The pattern of CDA modulations observed for the primary and secondary modalities were very similar to the results of Experiment 1a; see Fig. 2. For the primary tactile WM task, tCDA components reversed polarity in the S2 period on tactile shift trials, and this was the case not only in unimodal but also in bimodal blocks. Visual sample stimuli at S1 triggered CDA components in the bimodal task but not in the unimodal task when they were irrelevant. Importantly, visual CDAs observed during the S2 period in bimodal blocks did not change polarity on tactile shift trials.

Primary Modality (Touch, tCDA Components)

CSD values obtained during the delay periods following S1 and S2 were analyzed with the same statistical tests as in Experiment 1a. The amplitudes of tCDA components were reduced in bimodal as compared to unimodal blocks during the S1-period ('Task type': $t(15) = 2.801$, $P = 0.013$, $BF_{10} = 4.293$), as was found for the visual CDA in Experiment 1a. However, this tCDA amplitude difference between the 2 tasks was no longer present during the S2-period ('Task type': $F(1,15) = 0.006$, $P = 0.939$, $BF_{01} = 3.904$). As predicted, the tCDA reversed its polarity during the S2-period on tactile shift trials but not on tactile stay trials ('Trial type': $F(1,15) = 54.076$, $P < 10^{-5}$, $BF_{10} > 10^3$). Critically, there was no 'Task type' $\times$ 'Trial type' interaction ($F(1,15) = 0.016$, $P = 0.900$, $BF_{01} = 3.887$), demonstrating that this tCDA polarity reversal did not differ between the bimodal task where visual S1 sample stimuli on one side had to be maintained throughout, and

the unimodal task where visual samples could be ignored; see Figs 3B and 5.

These results were confirmed in a control analysis, where the S1-period baseline was subtracted from activity in the S2 period, as in Experiment 1a. There was a main effect for 'Trial type' ($F(1,15) = 60.670$, $P < 10^{-5}$, $BF_{10} > 10^4$), no significant effect for 'Task type' ($F(1,15) = 4.293$, $P = 0.056$, $BF_{10} = 1.379$), and importantly, no interaction between both factors ('Trial type' $\times$ 'Task type': $F(1,15) = 0.034$, $P = 0.856$, $BF_{01} = 3.856$).

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 2 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' $\times$ '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 Fig. 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' $\times$ '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, and were thus unrelated to the additional requirement to maintain visual sample stimuli on one side. WM accuracy for vision as secondary modality in the bimodal task did not differ between tactile shift and stay trials (92.3% vs. 92.6%; 'Trial type': $t(15) = 0.235$, $P = 0.818$, $BF_{01} = 3.8201$).

Experiment 2

To further scrutinize the apparent independence of the space-based attentional control of visual and tactile WM maintenance, Experiment 2 employed an orthogonal design where the presence versus absence of shifts between the task-relevant tactile or visual samples at S1 and S2 was manipulated independently for each modality. In addition, the visual WM task was changed relative to Experiment 1. As was the case for the tactile WM task, it now also involved the retention of spatial locations (see Fig. 1C). In Experiment 2, there were no unimodal blocks, and no distinction between primary and secondary modalities. On all trials, bimodal visual/tactile sample sets were presented at S1 and S2, and participants had to memorize task-relevant sample

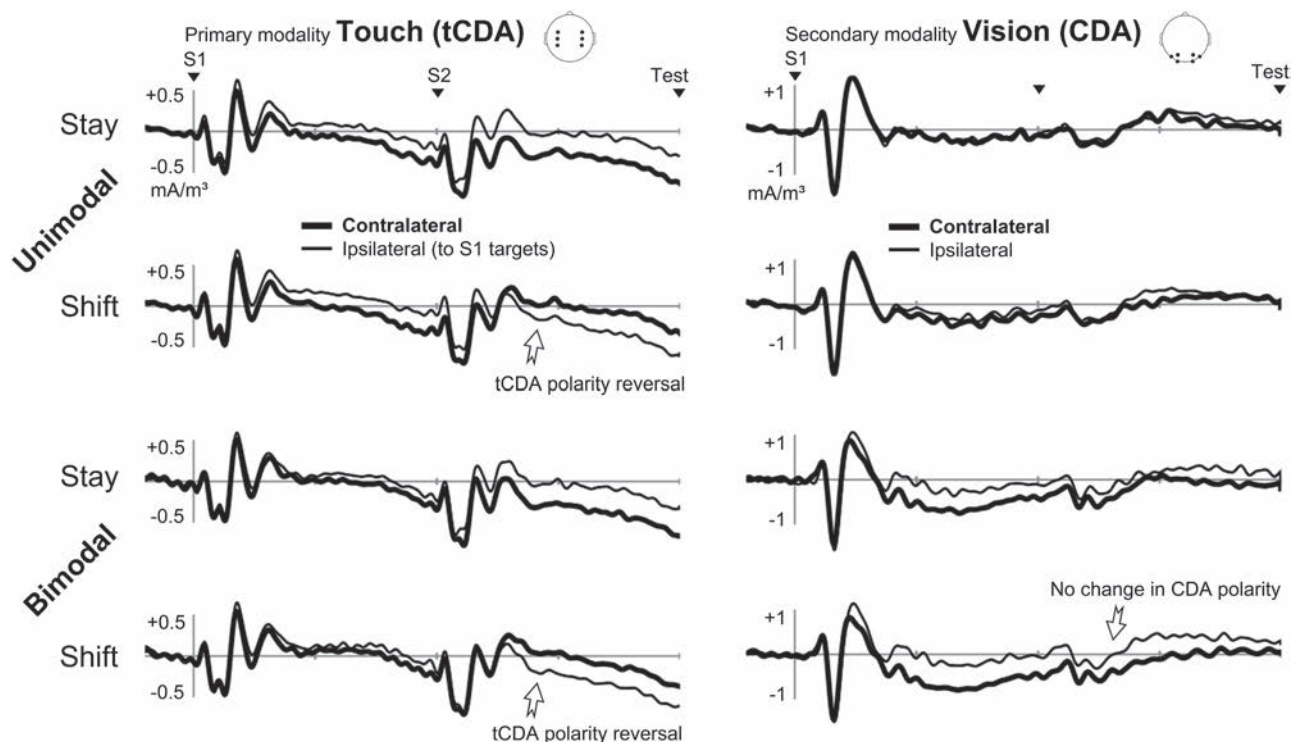


Figure 5. CSD amplitudes from Experiment 1b CSDs measured over somatosensory and visual areas contralateral and ipsilateral to task-relevant side of S1 sample sets in the unimodal and bimodal tasks. The tCDA reversed polarity during the S2 period on tactile shift trials in both tasks. There was no corresponding polarity change of visual CDA components in the bimodal task on tactile shift trials.

items on one side for each sample set. The visual and tactile S1 targets were always located on the same side, and this side remained constant within blocks. Visual and tactile S2 targets could appear on the same side or on the opposite side, and this was manipulated independently, resulting in 4 trial types (vision and touch stay; vision and touch shift; vision stay/touch shift; vision shift/touch stay).

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 Fig. 6 and the corresponding difference waveforms shown in Fig. 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 4 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 Fig. 7. Difference values obtained during the S1 and S2 periods were submitted to separate 3-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' $\times$ TT: $F(1,15) = 0.572$, $P = 0.461$, $BF_{01} = 3.048$; 'Component' $\times$ UT: $F(1,15) = 0.075$, $P = 0.787$, $BF_{01} = 3.787$; TT $\times$ UT: $F(1,15) = 1.976$, $P = 0.180$, $BF_{01} = 1.710$; 'Component' $\times$ TT $\times$ UT: $F(1,15) = 0.101$, $P = 0.755$, $BF_{01} = 3.743$). There was a main effect of 'Component' during the S1 period ($F(1,15) = 5.254$, $P = 0.037$, $BF_{10} = 1.911$), reflecting the known fact that CDA amplitudes were generally larger than tCDA amplitudes (e.g., Katus and Eimer 2018a).

During the S2 period, a main effect of 'Tracked Trial type' (TT: $F(1,15) = 42.116$, $P < 10^{-5}$, $BF_{10} > 10^4$) was present, reflecting a polarity reversal of the visual CDA component on visual shift trials, and of tactile CDA components on tactile shift trials; see Figs 6 and 7. Critically, there was no main effects or interactions involving the factor 'Untracked Trial type' (UT: $F(1,15) = 0.058$, $P = 0.813$, $BF_{01} = 3.815$; TT $\times$ UT: $F(1,15) = 0.230$, $P = 0.638$, $BF_{01} = 3.536$; 'Component' $\times$ UT: $F(1,15) = 1.033$, $P = 0.326$, $BF_{01} = 2.507$; 'Component' $\times$ TT $\times$ UT: $F(1,15) = 0.119$, $P = 0.735$, $BF_{01} = 3.713$). This demonstrates that the visual CDA was unaffected by the presence or absence of shifts in touch, and that the tactile CDA was not sensitive to the difference between visual stay versus switch trials. There was no significant main effect of 'Component' in the S2 period ($F(1,15) = 0.873$, $P = 0.365$, $BF_{01} = 2.681$), but there was an interaction between 'Component'

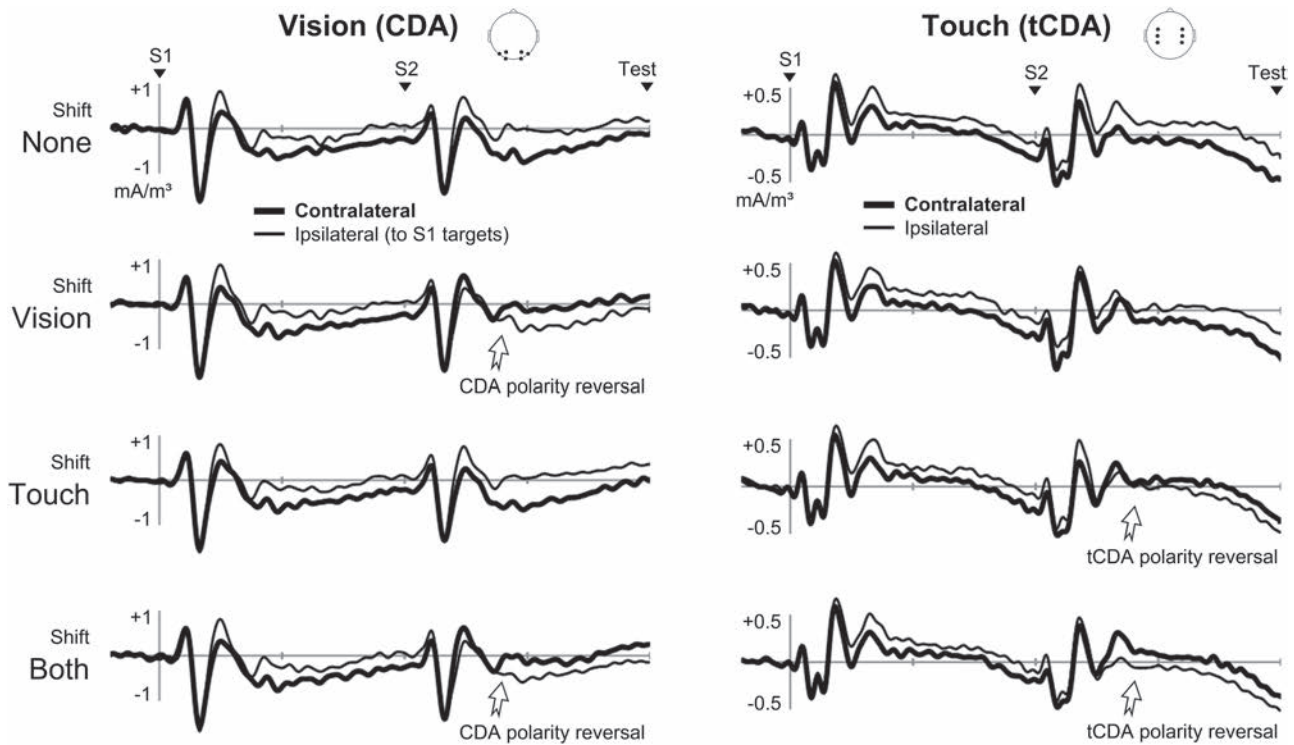


Figure 6. CSD amplitudes from Experiment 2 visual and somatosensory CDA components recorded contra- and ipsilateral to task-relevant sample items in S1, shown separately for trials with a S1–S2 target location shift in neither modality, in vision only, touch only, or in both modalities. Visual and tactile CDA components reversed polarity in the S2-period on visual and tactile shift trials, respectively, but were unaffected by shifts in the other untracked modality. Note the different scales for visual and tactile CSDs.

and TT ($F(1,15) = 9.755$, $P = 0.007$, $BF_{10} = 7.370$). This interaction reflects the fact that CDA amplitude differences between visual stay versus shift trials were larger than the corresponding tCDA amplitude differences between tactile stay and shift trials; note the different scales for tCDA/CDA components in Fig. 7. Due to the absence of any differential effects of TT or UT during the S1 period in Experiment 2 (see above), no additional control analyses with S1-period baselines were conducted for CDA amplitudes following S2.

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 $\times$ UT: $F(1,15) = 0.196$, $P = 0.665$, $BF_{01} = 3.589$). Further effects were non-significant

(TT $\times$ UT $\times$ ‘Tested modality’: $F(1,15) = 0.042$, $P = 0.841$, $BF_{01} = 3.842$; TT $\times$ ‘Tested modality’: $F(1,15) = 2.702$, $P = 0.121$, $BF_{01} = 1.292$; UT $\times$ ‘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 involving TT or UT (all P s > 0.05), indicating that attention shifts in either modality had no impact on memory for S2 items. For correct rejection rates, no significant effects were found (P s > 0.05).

Discussion

To examine the flexibility of space-based attentional control mechanisms in multimodal WM, we employed sequential loading procedures in bimodal visual/tactile WM tasks, and measured visual and tactile CDA components as ERP markers of the attentional activation of WM representations in modality-specific visual and somatosensory brain regions. On each trial, 2 memory sample sets (S1/S2) were presented sequentially, and the critical manipulation was whether the S1 and S2 targets in

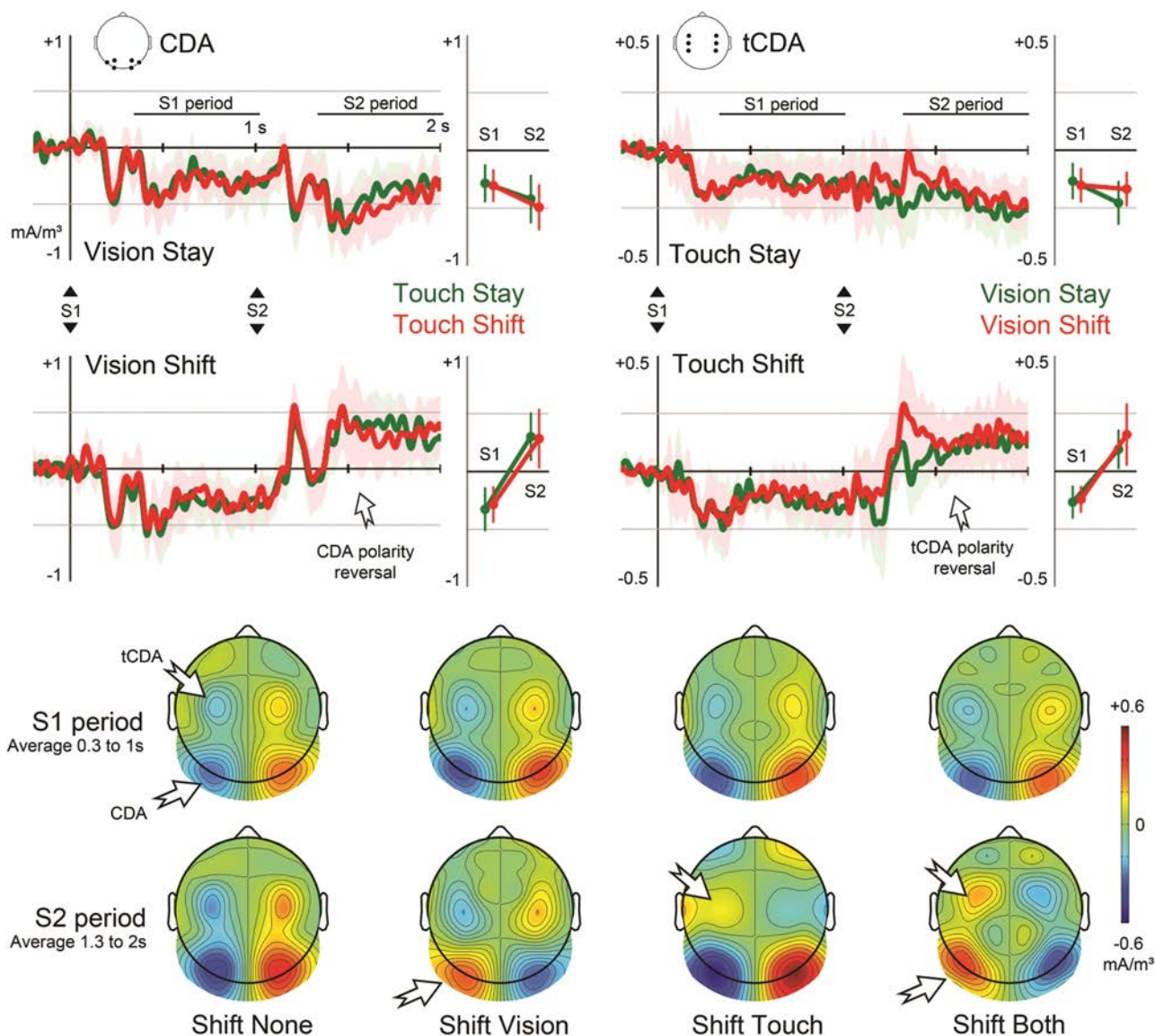


Figure 7. Contra-ipsilateral difference waves from Experiment 2. The left panel shows visual CDA components elicited on visual stay and shift trials, separately for trials where the position of tactile targets in S1 and S2 remained the same or changed (Touch Stay vs. Touch Shift). The right panel shows the corresponding tactile tCDA components for tactile stay and shift trials (Vision Stay vs. Vision Shift). The line graphs show mean tCDA/CDA amplitudes in the S1 and S2 periods of all 4 trial conditions. Error bars/shadings indicate CIs; note the different scales for the tCDA and CDA. Topographical maps show the distribution of lateralized delay activity during the S1 and S2 periods (top and bottom panels) for the 4 trial types.

a given modality were located on the same side or on opposite sides (stay vs. shift trials).

Experiment 1 included unimodal baseline conditions where only primary-modality stimuli (vision in Experiment 1a, touch in Experiment 1b) were task-relevant and S1 sample sets in the other modality could be ignored. In these unimodal WM tasks, visual and tactile CDA components were elicited contralateral to S1 targets in the S1 period and then reversed polarity during the S2 period on shift trials. This confirms previous observations from unimodal tactile and visual sequential loading experiments (Katus and Eimer 2015; Berggren and Eimer 2016), and indicates that spatial attention was reallocated to the location of S2 targets during the second delay period. In these 2 unimodal baseline tasks, there were no reliable CDA components over visual areas in blocks where visual sample stimuli had to be

ignored, and no significant tCDA components over somatosensory areas in blocks where 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 et al. 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 $\times$ 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 toward S2 targets on shift trials. Exactly the same pattern of CDA results was observed in Experiment 1b, where the roles of vision 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 primary modality had no impact on the polarity and amplitudes of CDA components for the secondary modality (touch in Experiment 1a, vision in Experiment 1b). This demonstrates that the constant focus of spatial attention during the maintenance of WM representations in the secondary modality remained unaffected by the presence versus absence of attention shifts during the S2 period in the primary WM task.

In line with this apparent independence of space-based attentional control mechanisms in visual and tactile WM, there were also no differences in WM performance between bimodal shift and stay trials in Experiment 1. In particular, accuracy on trials where WM for the secondary modality was tested was unaffected by whether primary modality S1 and S2 targets were presented on the same or on opposite sides. In other words, the maintenance of tactile or visual S1 samples was not impaired when the attentional focus in the other modality had to be re-allocated to the opposite side during the S2 period.

There was, however, a general bimodal cost for WM performance in Experiment 1. Accuracy for the WM task in the primary modality was higher in unimodal baseline blocks relative to bimodal blocks, and this was the case both for vision in Experiment 1a and for touch in Experiment 1b. These bimodal performance costs are in line with observations from previous behavioral studies (e.g., [Saults and Cowan 2007](#); [Fougnie and Marois 2011](#)), and they were accompanied by corresponding CDA differences between unimodal and bimodal blocks. Visual and tactile CDA/tCDA amplitudes for the primary tasks in Experiments 1a and 1b were smaller in bimodal blocks where secondary modality sample items had to be maintained concurrently relative to unimodal blocks where these items could be ignored (Task type main effect). These findings are consistent with a previous EEG experiment ([Katus and Eimer 2018b](#)) where CDA amplitudes elicited during visual WM maintenance were generally smaller when this task was performed concurrently with a tactile WM task, relative to a single-task baseline condition. This CDA attenuation in the bimodal task was interpreted as a result of the increased demands on central executive dual-task coordination mechanisms, and thus as a limitation in the concurrent top-down control of multiple WM maintenance processes in different modalities. Importantly, dual-tasking attenuated visual CDA amplitudes by the same amount regardless of WM load in the visual task, and visual load had no impact on tactile CDA amplitudes elicited during the maintenance of tactile items in the bimodal task. These

observations suggest that these bimodal costs are unrelated to the capacity of sensory storage mechanisms (see [Katus and Eimer 2018b](#), for further discussion). To eliminate amplitude differences between bimodal and unimodal task conditions during the S1 period, we ran additional analyses of tCDA/CDA components elicited in the S2 period after subtracting out tCDA/CDA amplitudes in the S1 period. This new baseline confirmed the absence of any Task type $\times$ Trial type interactions in Experiments 1a and 1b, as indicated by Bayesian analyses for both experiments. This result further underlines the independence of modality-specificity attentional control processes in visual and tactile WM, and demonstrates that this independence was unrelated to the dual-task coordination costs that accounted for reduced tCDA/CDA amplitudes in bimodal blocks during the S1-period.

In Experiment 1, attention shifts in the primary modality that took place during the S1-period had no impact on the stable focus of attention within the secondary modality that was already established during the S1-period. In Experiment 2, the necessity to shift attention between S1 and S2 or to maintain an attentional focus on the same side was orthogonally manipulated for visual and tactile WM, resulting in trials requiring attention shifts in one modality, neither modality, or in both modalities simultaneously. In contrast to Experiment 1, where participants memorized colors for the visual task and locations for the tactile tasks, memory for spatial locations was required for both tasks in Experiment 2. This change was introduced to maximize the representational overlap between both modalities (see [Tamber-Rosenau and Marois 2016](#), Exp. 8 in [Fougnie et al. 2015](#)), and to test whether the independent attentional control of visual and tactile WM found in Experiment 1 was linked to the fact that different types of information (spatial vs. featural) had to be maintained in different modalities (cf., [Zimmer 2008](#)). As in Experiment 1, visual CDA and CDA components initially emerged contralateral to the S1 targets. During the S2-period, the polarity of these CDA components was determined exclusively by the location of S2 target sample items in the corresponding modality, and was entirely unaffected by whether targets in the other untracked modality required a shift of spatial attention or not; see [Fig. 6](#). The polarity of the visual and tactile CDAs reversed on visual or tactile shift trials but not on visual or tactile stay trials, respectively (TT: Tracked Trial type main effect; see topographical maps in [Fig. 7](#)). Crucially, whether an attention shift was or was not required within one modality during the S2-period had no impact on the amplitudes of CDA components associated with the other modality (UT: Untracked Trial type main effect). There was also no evidence for any interactions between these 2 factors.

The behavioral results of Experiment 2 also demonstrated that WM maintenance in vision and touch was not affected by the spatial relationship between S1 and S2 targets in the other modality. WM accuracy for the modality that was tested did not differ between trials with versus without a location shift of S1 and S2 targets in the other untested modality. The reliability of all critical null effects for CDA/tCDA amplitudes and WM performance was confirmed with Bayesian tests. Overall, these results of Experiment 2 provide additional clear evidence for the independence of space-based attentional control mechanisms in visual and tactile WM.

What do the observations of the present study imply for the architecture of multimodal WM and its top-down control? The dynamic shifts of spatial attention between WM representations and hemispheres that were observed in this and

previous sequential loading studies, as well as in experiments on multiple object tracking (Drew et al. 2014a) could reflect the flexible updating of location pointers, which control the activation profile of WM representations in modality-specific visual or tactile spatial maps. The existence of such location pointers was initially proposed as a mechanism for visual stability during saccadic eye movements (Cavanagh et al. 2010) and for the online tracking of visual objects (Oksama and Hyona 2008). The visual indexing theory (Pylyshyn 1989) proposes that objects are tracked via their locations using spatial indices that convey no featural information about object identity. Similar pointer mechanisms could also be employed during the space-based attentional control of WM maintenance. This hypothesis is compatible with accounts proposing a map-based organization of WM (Franconeri et al. 2013), where information is stored as hierarchical feature bundles (Brady et al. 2011) in distributed 2D content maps. Objects in different sensory modalities are stored in feature maps in modality-specific sensory areas, as suggested by the sensory recruitment hypothesis of WM (Jonides et al. 2005). Because maps in higher-level attentional control areas, such as prefrontal cortex, lack sensitivity to low-level properties of stimuli (Thompson and Bichot 2005; Serences 2016), they may instead provide the spatial pointer mechanisms that are necessary to select particular items in WM in a top-down fashion. Such spatial indexing mechanisms for individual memorized objects are particularly important if features of these objects were represented in distributed modality-specific cortical maps. In this context, the emergence of visual and tactile CDA component observed in the present study could reflect the activation of WM representations in visual and tactile maps that is triggered by top-down input from spatial pointers, and the polarity reversal of these components on shift trials, the result of spatial updating processes within the location pointer system. Our results suggest that spatial indexing occurs in parallel and independently for objects stored in visual and tactile maps, allowing for strictly modality-specific dynamic changes in the allocation of attention during WM maintenance.

Conclusion

Top-down control processes regulate the activation of representations in sensory WM stores, and these processes operate in a dynamic and spatially selective fashion. The maintenance of visual and tactile items is mediated by spatial pointer mechanisms that specify the location of these items once they have been encoded into WM. The independence of attention shifts within visual and tactile WM indicates that the spatial indexing of somatotopic and retinotopic information is mediated by parallel modality-specific processes that operate in distributed cortical maps.

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