Behavioral/Cognitive

Sustained Maintenance of Somatotopic Information in Brain Regions Recruited by Tactile Working Memory

Tobias Katus,[1,2] **Matthias M. Müller,**[2] **and Martin Eimer**[1]

[1]Department of Psychology, Birkbeck College, University of London, London WC1E 7HX, United Kingdom, and [2]Institut für Psychology, Universität Leipzig, 04109 Leipzig, Germany

To adaptively guide ongoing behavior, representations in working memory (WM) often have to be modified in line with changing task demands. We used event-related potentials (ERPs) to demonstrate that tactile WM representations are stored in modality-specific cortical regions, that the goal-directed modulation of these representations is mediated through hemispheric-specific activation of somatosensory areas, and that the rehearsal of somatotopic coordinates in memory is accomplished by modality-specific spatial attention mechanisms. Participants encoded two tactile sample stimuli presented simultaneously to the left and right hands, before visual retro-cues indicated which of these stimuli had to be retained to be matched with a subsequent test stimulus on the same hand. Retro-cues triggered a sustained tactile contralateral delay activity component with a scalp topography over somatosensory cortex contralateral to the cued hand. Early somatosensory ERP components to task-irrelevant probe stimuli (that were presented after the retro-cues) and to subsequent test stimuli were enhanced when these stimuli appeared at the currently memorized location relative to other locations on the cued hand, demonstrating that a precise focus of spatial attention was established during the selective maintenance of tactile events in WM. These effects were observed regardless of whether participants performed the matching task with uncrossed or crossed hands, indicating that WM representations in this task were based on somatotopic rather than allocentric spatial coordinates. In conclusion, spatial rehearsal in tactile WM operates within somatotopically organized sensory brain areas that have been recruited for information storage.

Key words: **electroencephalography; event-related potentials; selective attention; somatosensation; working memory**

Introduction

In the year of its 40th birthday, the most influential structural account of working memory (WM; Baddeley and Hitch, 1974) still lacks a distinct memory module for the retention of tactile information. Recently, Baddeley (2012) hypothesized that tactile information may converge onto the storage component for visual information, the visuospatial sketchpad. Storing tactile locations in a nontactile format would require the recoding of anatomically referenced (somatotopic) coordinates into a modality-independent (allocentric) reference frame. Perceptual studies that used purely tactile (Soto-Faraco and Azañón, 2013) or cross-modal tactile–visual paradigms (Azañón and Soto-Faraco, 2008) revealed evidence for such a remapping process, which is automatically triggered by tactile stimulation (Azañón et al., 2010). Remapping computes allocentric coordinates for stimuli based on their locations on the skin and the current posture of the body.

Sensory recruitment accounts of WM (Pasternak and Greenlee, 2005; D'Esposito, 2007) assume that somatosensory brain areas store locations in a modality-specific (somatotopic) format. Visual and tactile WM rely on distributed neural networks that include prefrontal cortex (PFC; Romo and Salinas, 2003; Kostopoulos et al., 2007) and modality-specific perceptual areas (Zhou and Fuster, 1996; Harrison and Tong, 2009). According to the sensory recruitment model, memory traces are stored in sensory brain areas, whereas PFC performs top-down control functions that guide the goal-dependent modulation of WM representations (Lepsien and Nobre, 2006; Postle, 2006). Support for sensory recruitment comes from event-related potential (ERP) studies of visual WM that identified a sustained negativity [contralateral delay activity (CDA)] at posterior electrodes contralateral to the side of memorized objects during the retention period (Vogel and Machizawa, 2004). A tactile CDA (tCDA) component was recently found over somatosensory areas contralateral to the hand where tactile information was memorized (Katus et al., 2014b). The tCDA component is sensitive to tactile memory load and individual differences in working memory capacity and indexes the sustained spatial rehearsal of tactile information.

The present experiment investigated whether spatially selective maintenance processes in tactile WM operate within an allo-

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Correspondence should be addressed to Matthias M. Müller, Institut für Psychologie, Universität Leipzig, Neumarkt 9-19, 04109 Leipzig, Germany. E-mail: m.mueller@rz.uni-leipzig.de.

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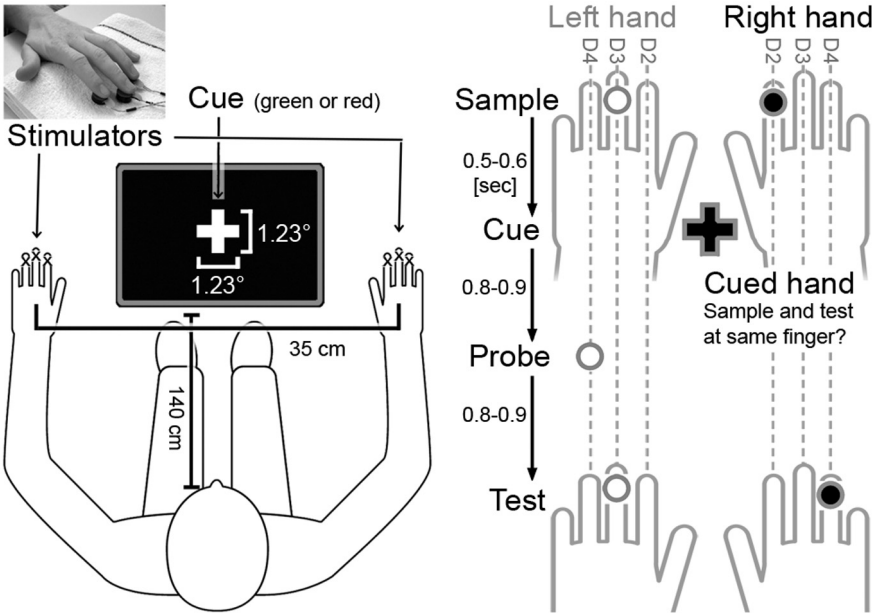

Figure 1. Stimulus material and task design. Top left, Six tactile stimulators were attached to the distal phalanges of the index (D2), middle (D3), and ring (D4) fingers of the left and right hands. Two sample stimuli were presented simultaneously to one finger of the left and right hands. A visual retro-cue signaled which of these two stimuli had to be retained and compared with the location of a subsequent test pulse at the same hand. The cue was followed by a task-irrelevant unilateral tactile probe and task-relevant bilateral test stimuli. In the example (shown for a block with uncrossed hand posture), the retro-cue indicates that the sample stimulus on the right hand has to be memorized, and the test stimulus presented to this hand does not match the location of the sample.

centric or somatotopic reference frame. Participants encoded two tactile sample stimuli simultaneously presented to the left and right hands, before a visual retro-cue indicated which of these stimuli had to be matched with a subsequent tactile test stimulus (Fig. 1). Retro-cues were presented between 500 and 600 ms after the samples to allow for the remapping of somatotopic coordinates into allocentric space (cf. Azañón and Soto-Faraco, 2008). We contrasted spatial rehearsal of cued tactile information in WM (indexed by the tCDA component) when allocentric and somatotopic coordinates were aligned (uncrossed hands) or in conflict (crossed hands). If rehearsal is based on modality-specific somatotopic WM representations, hand posture should not influence tCDAs elicited by retro-cues. If it operates within a modality-independent allocentric reference frame, tCDA components elicited by retro-cues should reverse polarity when hand posture is changed. To examine the role of focal spatial attention during spatially selective tactile WM maintenance and its link to hand posture, we also measured attentional modulations of somatosensory ERPs to task-irrelevant tactile probes and to the subsequent test stimuli.

Materials and Methods

Participants. Twenty neurologically unimpaired adult participants were tested (14 female; mean age, 23 years; range, 19–34 years). All participants were right-handed, gave informed written consent before testing, and received money or course credit. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethical committee.

Stimuli and task design. Participants were seated in a dimly lit recording chamber with their hands covered from sight. Six tactile stimulators were attached to the distal phalanges of the index, middle, and ring fingers of the left and right hands. Stimulators were driven by a dual-channel amplifier controlled by custom-written MATLAB scripts (The MathWorks) running on a Windows XP computer. White noise masked sounds produced by tactile stimulation. All tactile stimuli (sample, probe, and test stimuli) were mechanical pulses (duration, 5 ms; intensity, 0.37N). Visual stimuli (retro-cues) were centrally presented on a monitor (Fig. 1).

Each trial started with the presentation of a bilateral pair of tactile sample stimuli, which was followed by a visual retro-cue, a unilateral tactile probe stimulus, and a pair of bilateral tactile test stimuli (Fig. 1). Two sample pulses (one per hand) were simultaneously presented to one randomly selected finger of the left hand and one randomly determined finger of the right hand. The visual retro-cue was presented at a randomly determined time point between 500 and 600 ms after sample stimulus onset on the computer monitor by changing the white fixation cross to green or red (duration of color change, 150 ms). The color of the retro-cue indicated whether the tactile memory matching task had to be performed for the left or right hand. The color–hand assignment remained constant for each participant and was counterbalanced across participants. A unilateral task-irrelevant tactile probe stimulus was presented between 800 and 900 ms after the onset of the retro-cue, with equal probability to one of the six possible tactile locations on the left and right hands. At 800–900 ms after the probe, a bilateral pair of tactile test stimuli was presented to the left and right hands. On match trials, the test pulse on the cued (relevant) hand was presented to the same finger that had received the sample pulse. On mismatch trials, the test pulse on the cued hand was delivered to one of the two fingers that were not stimulated by the sample pulse. Match and mismatch trials were equally likely (50%). The location of the test pulse on the uncued (irrelevant) hand was determined in a fashion analogous to the cued hand. Because the randomization was performed for each hand separately, locations of test pulses were not correlated between the cued and uncued hands.

Participants were instructed to initially encode both tactile sample stimuli and then to decide on each trial whether sample and test stimulus locations on the hand indicated by the retro-cue matched or did not match. They signaled a match or mismatch with a vocal response ("a" for match, "e" for mismatch) recorded by a microphone. The response period (duration, 2600 ms) was indicated by a question mark that appeared on the monitor 400 ms after test stimulus onset. In alternating blocks, this task was performed with uncrossed or crossed hands. Hand posture in the first experimental block was counterbalanced across participants.

The experiment consisted of 10 blocks. Each block contained 56 trials and took about 5 min to complete. Performance feedback was given after each block. Participants performed an equal number of training trials with uncrossed and crossed hand posture (80–120 trials for each posture, dependent on participants' performance during training). They were asked to avoid head and arm movements and to maintain gaze fixation during EEG recordings. Task instructions emphasized accuracy over speed.

Data recording and analysis. EEG data, sampled at 256 Hz using a Biosemi ActiveTwo amplifier, were recorded from 64 Ag/AgCl active electrodes at standard locations of the international 10-10 system. A bipolar outer canthus montage [horizontal electro-oculogram (HEOG)] monitored lateral eye movements; a montage below and above the right eye (vertical electro-oculogram) monitored vertical eye movements and blinks. Continuous EEG data were referenced to the arithmetic mean of both mastoids and submitted to a digital 40 Hz low-pass finite impulse response filter (Blackman window, filter order 666). ERP epochs were computed for the 1800 ms interval after the visual retro-cue, for the 300 ms interval after the tactile probe stimulus, and for the 500 ms interval

after the tactile test stimuli, and these epochs were corrected relative to the 100 ms prestimulus baselines.

Blind source separation of EEG data was performed with the Independent Component Analysis (ICA) algorithm implemented in the EEGLab toolbox (Delorme and Makeig, 2004). Independent components related to eye blinks, vertical and horizontal eye movements were identified by visual inspection and subtracted from EEG sets (Delorme et al., 2007). On average, 2.3% of epochs contained lateral eye movements, as indicated by a differential step function running on the bipolarized HEOG (step width, 100 ms; threshold, 24 μV). None of these epochs was marked for rejection by the same function after ICA was used to correct for lateral eye movement artifacts. Epochs entered FASTER (Fully Automated Statistical Thresholding for EEG Artifact Rejection; Nolan et al., 2010) and were visually rechecked. Approximately 90.7% of all epochs to retro-cues, 92.6% of all epochs to probes, and 92.2% of test stimulus epochs were retained for statistical analysis. Analyses included trials with correct and incorrect responses to maximize the signal-to-noise ratio. The exclusion of incorrect trials yielded an identical pattern of results for all measures of interest.

ERP waveforms were separately averaged across six lateral electrodes (FC3/4, FC5/6, C3/4, C5/6, CP3/4, CP5/6) over somatosensory brain areas contralateral and ipsilateral to the currently task-relevant hand. Statistical tests were conducted on mean amplitudes for the time windows of respective ERP components (see below). Data shown in spline-interpolated topographical voltage maps were collapsed across trials in which the left or right hand was task relevant by flipping electrode coordinates in trials with left-hand cues over the midline. Error bars in graphs showing difference values reflect 95% confidence intervals that were calculated for each condition by t tests against zero (i.e., no difference). Statistical significance of difference values is symbolized by asterisks ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$) and is marked by error bars that do not overlap with the zero axis.

Onset latency differences between tCDA components in blocks with uncrossed versus crossed hands were assessed with a jackknife-based procedure (Miller et al., 1998). Twenty grand-average difference waves were computed for both hand posture conditions, each excluding one different participant from the original sample, and tCDA onset latency was defined as the point in time when each subsample difference wave reached an absolute onset criterion of -0.3 μV. Onset latency differences between the two conditions were tested with a two-tailed t test, with the t value corrected according to the formulas described by Miller et al. (1998).

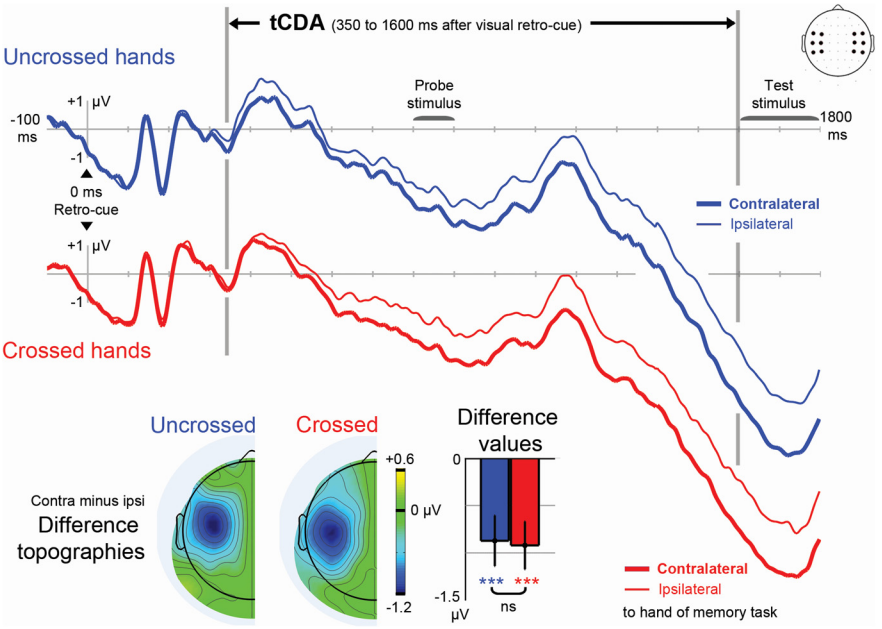

Figure 2. ERPs elicited in response to visual retro-cues during the 1800 ms interval until the presentation of the bilateral test stimuli, at electrodes contralateral (bold lines) and ipsilateral (thin lines) to the hand specified as task relevant by the retro-cue, are shown separately for blocks with uncrossed (blue) and crossed (red) hand posture. Bottom left, The difference maps show the topographical distribution of lateralized activity in the tCDA time window (350–1600 ms after retro-cue onset) in blocks with uncrossed and crossed hands. These maps represent the amplitude difference of contralateral minus ipsilateral ERP waveforms, collapsed across trials where the left hand or right hand was relevant for the memory matching task. Bottom right, The bar graph shows contralateral minus ipsilateral difference amplitudes for the tCDA time window in blocks with uncrossed (blue) and crossed (red) hand posture. Error bars reflect 95% confidence intervals of conditional difference values tested against zero (i.e., no lateralized effect). Hand posture had no effect on tCDA amplitudes.

Results

Delay period activity evoked by retro-cues

Visual retro-cues were presented 500–600 ms after the tactile sample set and indicated whether the left- or right-hand sample pulse had to be selectively maintained. To determine whether selective attention to one of the two stimuli in tactile working memory would trigger sustained maintenance-related delay period activity over contralateral somatosensory cortex, difference waveforms were calculated by subtracting ERP traces recorded ipsilateral to the cued hand from contralateral ERPs, and statistical analyses were conducted on mean difference amplitudes measured for the tCDA component time window (from 350 ms after retro-cue onset until 1600 ms, i.e., the onset of bilateral test pulses) across the six lateral central electrode pairs. The presence of reliable lateralized effects is marked by difference values that significantly deviate from zero.

Retro-cues elicited a sustained negativity (tCDA component) over somatosensory scalp regions contralateral to the relevant (cued) hand. As shown in Figure 2, tCDA components emerged around 350 ms after retro-cue onset and remained present throughout the remaining delay period. Statistically reliable tCDAs were present in blocks with uncrossed ($t_{(19)} = -6.439$, $p < 10^{-5}$) and crossed ($t_{(19)} = -7.166$, $p < 10^{-6}$) hand posture. The size of the tCDA component did not differ between blocks with uncrossed and crossed hand posture ($p > 0.7$), demonstrating that the maintenance-related activity reflected by this component was determined by anatomical rather than allocentric coordinates of the memorized stimulus. However, as can be seen in Figure 2, the tCDA emerged slightly earlier when hands were uncrossed. An analysis of tCDA amplitudes during the 350–500 ms interval after retro-cue onset confirmed this observation. A reliable tCDA was already present during this early interval with uncrossed hand posture ($t_{(19)} = -3.654$, $p = 0.002$) but not with crossed hands ($t_{(19)} = -1.452$, $p = 0.163$). The delay of the tCDA with crossed hands was formally assessed with a jackknife-based procedure (Miller et al., 1998). The tCDA emerged 335 ms after retro-cue onset with uncrossed hands and 426 ms after cue onset with crossed hands. This onset latency difference of 91 ms was significant ($t_{(19)} = 4.431$, $p < 0.001$; proportion of explained variance $r^2 = 0.508$).

ERPs to tactile probe stimuli

Figure 3*A* shows ERPs elicited by tactile probes presented to the relevant hand at contralateral electrodes over somatosensory cor-

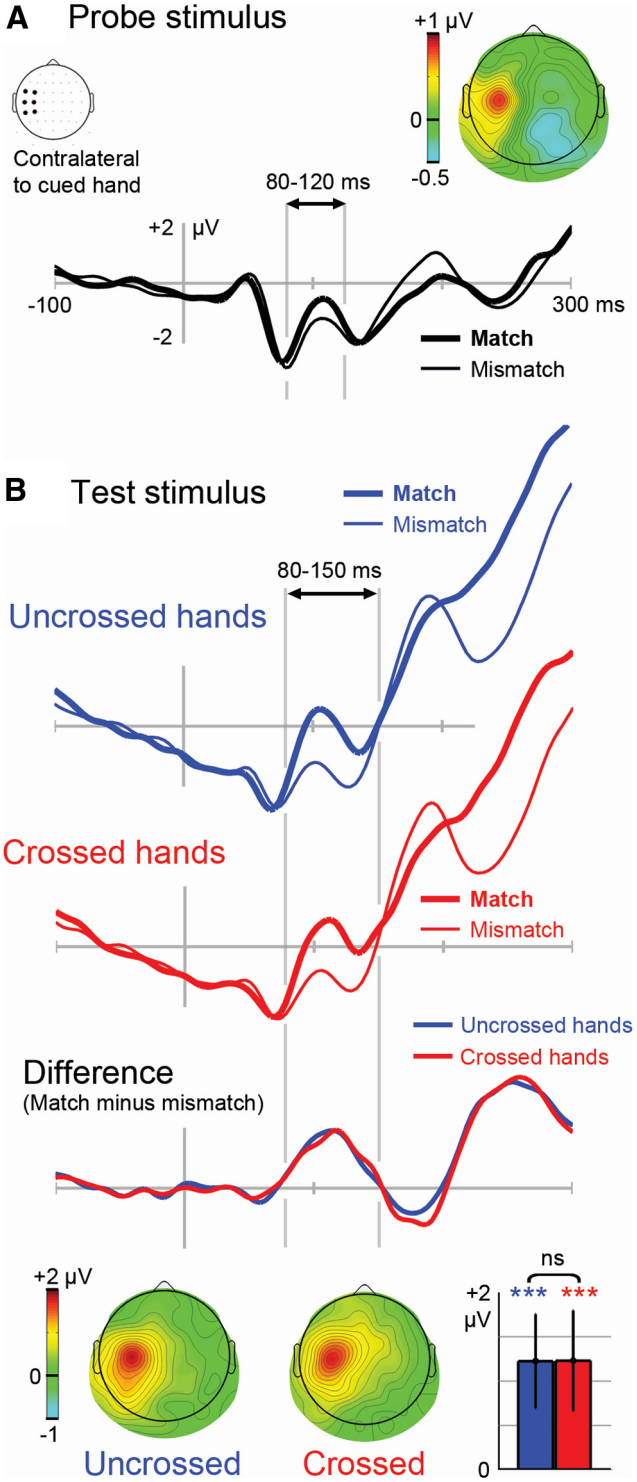

Figure 3. ***A***, ERPs elicited by tactile probe stimuli delivered to the task-relevant hand at electrodes contralateral to this hand during the 300 ms interval after probe onset, collapsed across blocks with uncrossed and crossed hands. ERPs are shown separately for trials where a probe was presented at the same finger as the memorized sample stimulus (match trials) and trials where the probe was delivered to another finger of the same hand (mismatch trials). The somatosensory P100 component was enhanced on match trials, and the map shows the topographical distribution of this P100 modulation on the basis of difference waves obtained by subtracting ERP mean amplitudes measured in the P100 time range (80–120 ms after probe onset) on mismatch trials from ERPs on match trials. ***B***, ERPs elicited by bilateral tactile test stimuli at electrodes contralateral to the task-relevant hand during the 300 ms interval after test onset, on match trials where the test stimulus was presented at the same finger as the memorized sample stimulus and on mismatch trials where it was delivered to another finger of the same hand. ERPs are shown separately for blocks with uncrossed and crossed hands. The somatosensory P100 component was enhanced on match trials, and this attentional modulation overlapped with the subsequent N140 component. The topographical maps show the distribution of this effect during the 80–150 ms interval after test stimulus onset. They were obtained by subtracting ERPs on mismatch trials from ERPs on match trials. Difference waves (match minus mismatch trials) show identical attentional modulations in blocks with uncrossed and crossed hands. Bar graphs show mean difference amplitudes at contralateral central electrodes. Error bars reflect 95% confidence intervals of difference values tested against zero.

tex, separately for probes presented to the finger that had received the to-be-memorized sample pulse and for probes presented to one of the fingers that were not stimulated by a sample pulse. The somatosensory P100 component was enhanced when probes were presented to the same finger that was stimulated by the preceding task-relevant sample pulse relative to probes presented to one of the other fingers of the same hand. A formal test of ERP mean amplitudes measured in a time window centered on the P100 component (80–120 ms after probe onset) obtained a reliable effect of probe location (memorized vs not memorized finger) on P100 amplitude ($F_{(1,19)} = 5.221$, $p = 0.034$). There was no significant main effect of hand posture (uncrossed vs crossed, $p > 0.4$) and no reliable hand posture × probe location interaction ($p > 0.6$).

ERPs to tactile test stimuli

After the retention period, tactile test stimuli to the cued task-relevant hand were either delivered to the same finger where a sample had been presented (match trial, 50%) or to a different finger (mismatch trial, 50%). Figure 3*B* shows ERPs triggered by test stimuli at electrodes recorded contralateral to the task-relevant hand on match and mismatch trials, separately for blocks with uncrossed and crossed hand posture. Similar to observations for tactile probes, the somatosensory P100 component was enhanced on match trials where a test stimulus was delivered to the same finger that had received the memorized sample pulse relative to mismatch trials where a different finger of the same hand was stimulated at test. In contrast to the probe stimulus results, this attentional modulation of somatosensory ERPs extended beyond the P100 component and also modulated the subsequent N140 component. To assess the reliability of this effect, mean ERP amplitudes at central electrodes contralateral to the task-relevant hand were computed within a time window that overlapped with the P100 component and N140 components (80–150 ms after stimulus). Significant differences between match and mismatch trials were present both with uncrossed hands ($t_{(19)} = 4.466$, $p < 0.001$) and with crossed hands ($t_{(19)} = 5.149$, $p < 10^{-4}$). The size of these attentional modulations did not differ between hand postures ($p > 0.8$).

Behavioral performance

Participants correctly reported a match or mismatch between tactile sample and test stimuli on the cued hand in 93.2% of all trials with uncrossed hands and in 86.0% of all trials with crossed hands. An analysis of sensitivity indices (d′) by a two-way repeated-measures ANOVA with the factors cued hand (left, right) and hand posture (uncrossed, crossed) confirmed that this effect of hand posture was reliable ($F_{(1,19)} = 26.335$, $p = 10^{-4}$). There was no significant main effect of cued hand and no hand posture × cued hand interaction.

Discussion

We examined spatial rehearsal in somatosensory brain areas using a tactile spatial WM task. Two bilaterally presented tactile

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sample stimuli first had to be encoded in parallel before a visual retro-cue indicated which of these stimuli had to be selectively maintained. Because the location of the target stimulus was not known before the retro-cue was presented, WM initially contained neural representations of tactile stimuli on both hands, unbiased by top-down control, in the period between sample set and retro-cue. The retrospective cueing procedure served to delay spatial rehearsal in WM to allow for a complete remapping of the tactile sample set into an allocentric reference frame (cf. Azañón and Soto-Faraco, 2008). In different blocks, the memory task was performed with uncrossed and crossed hand posture to selectively manipulate allocentric stimulus coordinates, which depend on whether a stimulated limb is located at the left or right side of the body. Electrophysiological data revealed that spatially selective WM maintenance processes in somatosensory brain areas are not sensitive to manipulations of body posture. This demonstrates that spatial rehearsal of tactile information operates within the somatotopically organized spatial layout of tactile WM in sensory brain areas that have been recruited for information storage.

Sustained rehearsal of task-relevant coordinates in somatotopic space

Retro-cues triggered a tCDA component over somatosensory cortex contralateral to the cued hand in both hand posture conditions (Fig. 2) and resulted in attentional processing enhancements for tactile probes and test stimuli that were presented at to-be-retained locations (Fig. 3). A previous study (conducted with uncrossed hands) has shown that the tCDA component emerges during the maintenance of tactile information when there is no conflict between allocentric and somatotopic reference frames (Katus et al., 2014b). The presence of a tCDA, contralateral to the cued hand when these reference frames were misaligned (crossed hands; Fig. 2), indicates that the tCDA reflects the sustained engagement of modality-specific control mechanisms that modulate the content of tactile WM in a goal-directed fashion through the spatially selective biasing of somatotopic representations in tactile WM.

The fact that tCDA components were very similar in size when participants performed the task with crossed or uncrossed hands provides additional evidence that the memory representations that were maintained in a spatially selective fashion were not stored in an allocentric format. Crossing the hands induces a conflict between anatomical and allocentric spatial coordinates, which can impair tactile judgments (Yamamoto and Kitazawa, 2001) and the attentional selection of tactile events (Eimer et al., 2003). Despite the robust reduction in behavioral performance when hands were crossed, the onset of the tCDA component was only moderately delayed by <100 ms, suggesting that a conflict of reference frames has a relatively small effect on somatosensory processes involved in the storage and maintenance of tactile information.

Spatial attention in tactile WM operates within a narrow focus of somatotopic space

Whereas the presence of tCDA components in response to visual retro-cues indicates different activation levels for the contralateral versus ipsilateral hemispheres during retention, this hemispherical asymmetry in neural processing does not provide more detailed insights into the spatial specificity of attentional modulations. Retro-cues might have triggered a shift of spatial attention toward the relevant hand, resulting in a global enhancement of processing in somatosensory cortex contralateral to the memorized hand. Alternatively, they may have elicited a more spatially selective attentional facilitation of tactile processing at somatotopic locations that matched the position of the memorized finger. The ERP results obtained in response to unilateral task-irrelevant probe stimuli delivered to the cued hand provide clear evidence for a narrow focus of spatial attention during tactile WM maintenance. These probes appeared 800–900 ms after the retro-cue and triggered an attentional enhancement of the somatosensory P100 component when they were presented to the location that had previously received the tactile sample stimulus, relative to probes that were presented to a different finger of the same cued hand (Fig. 3*A*). We recently compared ERPs for tactile probe stimuli presented at the cued hand with probes at the uncued hand and found an attentional modulation of the N140 component, indicating that the allocation of spatial attention was biased toward the hand where a location is memorized during retention (Katus et al., 2012). The modulation of the somatosensory P100 component at scalp regions contralateral to the hand where stimuli were memorized in the present study demonstrates that during the selective maintenance of a tactile stimulus at a particular location on the cued hand, spatial attention was focused on the exact location of this stimulus in somatotopic space [see Eimer and Forster (2003) and Heed and Röder (2010) for similar ERP effects in perceptual tactile attention tasks].

The pattern of ERP results obtained in response to bilateral tactile test stimuli (Fig. 3*B*) confirmed this conclusion. P100 components triggered at electrodes contralateral to the cued hand were enhanced on trials where a test stimulus matched the exact location of the sample stimulus on this hand, relative to trials where test stimuli appeared at a nonmatching location. This attentional enhancement of ERPs to test stimuli was similar to the corresponding modulation of probe ERPs (Fig. 3*A*) and overlapped with the subsequent somatosensory N140 component. For these stimuli, ERP modulations were virtually identical in blocks with uncrossed and crossed hand posture (Fig. 3*B*, difference wave), again demonstrating that somatosensory encoding was guided by mnemonic content referenced to somatotopic rather than allocentric space.

It is well established that the rehearsal of tactile and visual information in WM is mediated by qualitatively similar strategies, which involve covert spatial attention shifts to memorized locations [vision (Awh et al., 2006) and touch (Katus et al., 2012)]. Since visual locations are referenced to retinotopic or spatiotopic rather than somatotopic space, the neural implementations of these attention-based rehearsal mechanisms are obviously different for visual versus tactile information. This is in line with the sensory recruitment model that assumes that the WM maintenance of information from different sensory modalities is implemented in separate modality-specific memory systems.

No evidence for allocentric remapping during WM maintenance of tactile locations

The bulk of computations for tactile remapping are performed between 70 and 190 ms after stimulus [Soto-Faraco and Azañón, 2013; see Azañón and Soto-Faraco (2008) for evidence that remapping may extend up to 360 ms after stimulus]. Although remapping is ongoing, the concurrent presence of somatotopic and allocentric codes between 100 and 140 ms after stimulus (Heed and Röder, 2010) interferes with the spatial selection of perceptually presented stimuli and leads to reduced attentional modulations of the P100 and N140 components if somatotopic and allocentric reference frames are misaligned (Eimer et al., 2003). No such interference effects on somatosensory ERP com-

ponents were found here. These results seemingly suggest that our participants did not remap tactile stimuli to allocentric space, which would contradict previous findings that remapping occurs automatically in response to tactile stimulation (Gallace et al., 2008; Azañón et al., 2010). However, these studies also indicated that remapping can show a considerable degree of flexibility as the spatial reference frame adopted by participants critically depends on the specific demands of an experimental task. Such observations suggest that tactile processing is based on spatial representations that result from a weighted integration of somatotopic coordinates with postural information (de Haan et al., 2012). The dominance of somatotopic space during memory maintenance observed in the current experiment may thus reflect the high priority of somatotopic spatial coordinates in a task where successively presented tactile stimuli have to be spatially matched on the skin's surface. Future work needs to clarify the conditions under which allocentric coordinates and supramodal attentional control processes can affect spatially selective WM maintenance processes in somatosensory cortical regions.

Theoretical perspectives

Our findings contradict the assertion that tactile information is always automatically recoded into allocentric space and that this recoding is critical for the storage of tactile information within a nontactile memory system (e.g., the visuospatial sketchpad). They also highlight the need to include a dedicated storage component for somatosensory information within current structural models of WM (Baddeley, 2012). Our results support sensory recruitment accounts (Pasternak and Greenlee, 2005; Postle, 2006) that postulate that tactile WM emerges when selective attention is directed to memory traces, residing in somatosensory brain regions that were recruited for information storage. The information contained in this modality-specific, somatotopically organized storage system can be flexibly altered according to behavioral goals and is sustained by spatial rehearsal mechanisms that regulate the activation of tactile representations in somatosensory cortex. Spatial attention plays a central role as a rehearsal mechanism for visual (Awh et al., 2000) and tactile (Katus et al., 2014a) locations. Despite this apparent similarity across vision and touch, we show that spatial rehearsal of tactile information is mediated by distinct modality-specific control mechanisms that influence neural processing at the site where information is stored.

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