

# Common Mechanisms of Spatial Attention in Memory and Perception: A Tactile Dual-Task Study

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**Orienting attention to locations in mnemonic representations engages processes that functionally and anatomically overlap the neural circuitry guiding prospective shifts of spatial attention. The attention-based rehearsal account predicts that the requirement to withdraw attention from a memorized location impairs memory accuracy. In a dual-task study, we simultaneously presented retro-cues and pre-cues to guide spatial attention in short-term memory (STM) and perception, respectively. The spatial direction of each cue was independent of the other. The locations indicated by the combined cues could be compatible (same hand) or incompatible (opposite hands). Incompatible directional cues decreased lateralized activity in brain potentials evoked by visual cues, indicating interference in the generation of prospective attention shifts. The detection of external stimuli at the prospectively cued location was impaired when the memorized location was part of the perceptually ignored hand. The disruption of attention-based rehearsal by means of incompatible pre-cues reduced memory accuracy and affected encoding of tactile test stimuli at the retrospectively cued hand. These findings highlight the functional significance of spatial attention for spatial STM. The bidirectional interactions between both tasks demonstrate that spatial attention is a shared neural resource of a capacity-limited system that regulates information processing in internal and external stimulus representations.**

**Keywords:** attention, attention-based rehearsal, electroencephalography, short-term memory, somatosensation

## Introduction

Short-term memory (STM) refers to cognitive functions involved in the maintenance and/or manipulation of information contained in internal representations that endure for brief periods of time (Zimmer 2008). Evidence suggests that mnemonic representations are subject to top-down influence with considerable functional and anatomical overlap to the neural circuitry mediating spatial selection of external, that is, perceived or anticipated stimulus representations (Awh and Jonides 2001; Naghavi and Nyberg 2005; Pasternak and Greenlee 2005; Awh et al. 2006; Lepsien and Nobre 2006; Müller and Knight 2006; Sörös et al. 2007).

Spatial selection can be investigated through lateralized components of the event-related potential elicited by attention-directing cues. Lateralized components are spatially specific effects and represent amplitude differences across electrodes that are located contra- versus ipsilateral to the direction of attention shifts. Late lateralized components, such as the “anterior directing attention negativity” (ADAN) and “late directing attention positivity” (LDAP), are associated with executive processes residing at a high level in the

hierarchy of endogenous control, specifically, supramodal attention (Eimer and van Velzen 2002; van Velzen et al. 2002; Eimer et al. 2003; Jongen et al. 2007; Seiss et al. 2007). Most importantly, these components are equally sensitive to spatial selection in internal and external stimulus representations (e.g. Griffin and Nobre 2003). Such engagement of equivalent functions leads to the hypothesis that spatial selection in internal and external representations might be controlled by a unitary system rather than encapsulated modules that are specific to prospective versus retrospective shifts of spatial attention.

The attention-based rehearsal account proposes that spatial attention supports the maintenance of spatial STM (Awh and Jonides 2001; Awh et al. 2006; Theeuwes et al. 2009). Attention-based rehearsal rests on 2 key assumptions: First, spatial attention is directed toward memorized locations during the retention delay of spatial STM tasks (Awh et al. 2000; Jha 2002). Secondly, such spatial attention shifts represent adaptive strategies to optimize memory accuracy (Awh and Jonides 2001; Awh et al. 2006, but see also: Belopolsky and Theeuwes 2009b); this implies that the withdrawal of attention from memorized locations should impair memory accuracy. In line with the first tenet of attention-based rehearsal, we found attention shifts to memorized locations in a previous tactile STM experiment (Katus et al. 2012a). Uncertainty, however, exists regarding the second prediction: Does spatial attention have a functional significance for tactile STM for locations? The present dual-task study used a high-priority perceptual task to either allow or disrupt attention-based rehearsal in STM by means of forced attention shifts to external events. If shared neural mechanisms mediate spatial selection in STM and perception, interference should arise when retrospective and prospective attention shifts are directed to locations far apart rather than nearby.

The present study implemented a design in which participants performed a prioritized perceptual task during the retention delay of a memory task. Cue configurations were always predictive and consisted of a retro-cue (memory task) presented along with a pre-cue (perceptual task). Cues indicated the target location (hand) associated with the respective task. The direction of each cue varied independently of the other—cues were thus either compatible (same hand) or incompatible (different hands). Interferences reflecting the division of spatial attention between both hands should arise in the incompatible cue condition if both tasks rely on shared neural resources of spatial attention. Relative to the compatible condition, incompatible cues should attenuate lateralized components that are equally sensitive to retrospective and prospective shifts of spatial attention, such as ADAN and

LDAP. We further examined whether the somatosensory N140 and the “late positive component” (LPC; [Desmedt and Debecker 1979](#)) evoked by test stimuli of the memory task are sensitive to the disruption of attention-based rehearsal caused by directionally incompatible cues. Regarding the perceptual task, we assessed the LPC to transient events in vibrotactile streams and the “somatosensory steady-state evoked potential” (SSSEP). Spatially specific somatosensory encoding modulates the amplitude of the SSSEP ([Giabbiconi et al. 2007](#)) and also of the N140 component ([Forster and Eimer 2005](#)); the LPC reflects neural processing downstream to the somatosensory system ([Sambo and Forster 2011](#)). We expected a reduction of LPC and SSSEP amplitudes in incompatible cue trials, relative to the compatible cue condition.

## Materials and Methods

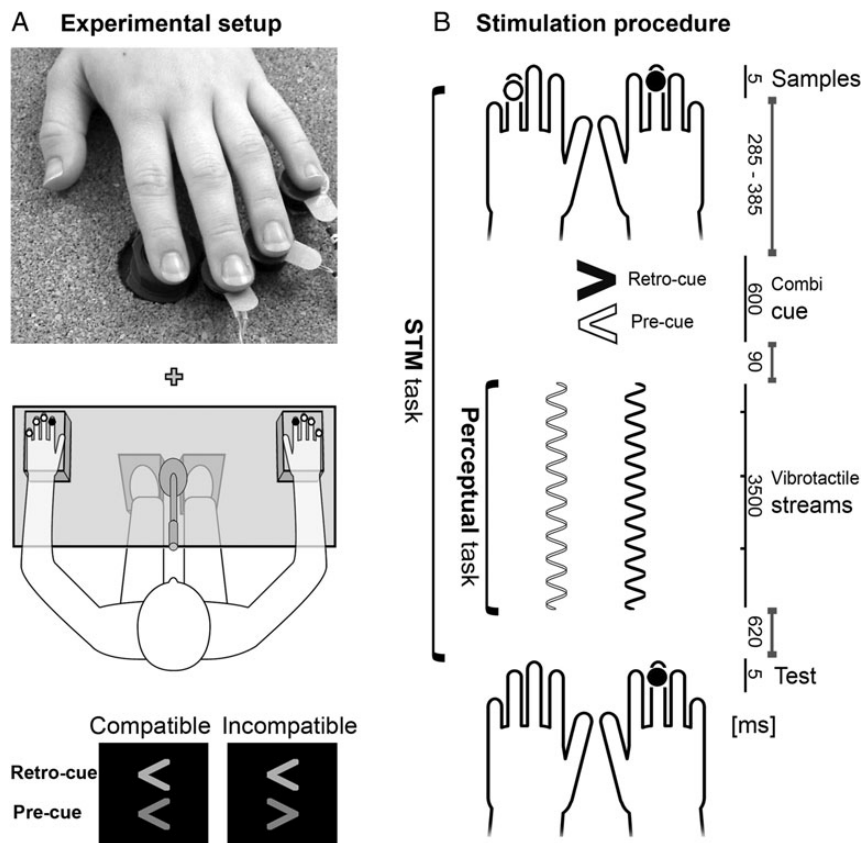
### Participants

Twenty-one subjects participated in the experiment; 3 were excluded prior to statistical analysis: 1 participant violated instructions by lifting the finger from the stimulator that delivered the to-be-ignored vibrotactile stream, as indicated by the complete absence of SSSEPs at the frequency of the prospectively uncued stream. A second subject was

excluded due to poor behavioral performance in both tasks. A third exhibited problems to maintain fixation and was also removed from the remaining sample of 18 participants (11 female, age range = 20–34 years, average = 24 years). All were right-handed according to the Edinburgh Handedness Inventory ([Oldfield 1971](#)), reported no history of neurological illness, and had normal or corrected-to-normal vision. Participants gave informed written consent and received payment or course credit. The experiment was conducted in accordance with the Declaration of Helsinki.

### Experimental Set-up

Figure 1 illustrates stimulator placement and experimental set-up. Tactile stimuli involved in the perceptual task were presented by modified loudspeakers (model: FR 10, 2020; Visaton, Haan, Germany), driving blunt plastic rods that contacted the skin of the index fingers. Additional electromagnetic stimulators (Dancer Design, St. Helens, United Kingdom) provided tactile stimuli involved in the memory task. These stimulators were adhered to the subject’s middle, ring, and small fingers of the left and right hands. Towels covered the subject’s hands and stimulators from sight. Distance between both hands was kept constant at approximately 80 cm. White noise was presented via headphones to mask any sounds produced by the stimulators. Stimulators received power supply by a dual-channel amplifier. A digital-to-analog conversion card served as an interface between computer and amplifier. Visual stimuli (e.g. the combined cues) were



**Figure 1.** (A) Experimental set-up and stimulation hardware. (Top) A hand equipped with 4 stimulators. Three stimulators were attached to the distal phalanges of D3, D4, and D5. A further device stimulated D2. (Middle) Vibrotactile streams related to the perceptual task were presented to the index fingers (black dots). The locations of concise pulses involved in the memory task were randomized (white dots). Visual stimuli were shown in the center of the monitor. Participants gave speeded foot button presses and delayed vocal responses in the perceptual and memory task, respectively. (Bottom) The visual cue configurations consisted of two simultaneously presented arrowheads that served as retro- and pre-cue. The arrowheads pointed in the same direction (compatible) or in opposite directions (incompatible). (B) Stimulation procedure. The visual cues succeeded presentation of bilateral tactile sample stimuli and preceded onset of vibrotactile streams. Subjects were instructed to detect transient irregularities (events) in the vibrotactile stream at the prospectively cued hand while memorizing a location at the retrospectively cued hand. Relative to stream onset, events were presented at 3 latencies (500, 1500, or 2500 ms). As to the memory task, test stimuli were delivered to the retrospectively cued hand, at a memorized (50%) or nonmemorized location (50%). In the illustrated example of an incompatible cue trial, the right hand was cued retrospectively (black) and the left hand prospectively (white).

visible through a window in the recording chamber and presented on a 19-inch cathode ray tube monitor at a distance of 140 cm relative to the subjects head. Stimulation was controlled by MATLAB (The Math-Works, Natick, United States of America), running on a Windows XP computer (Microsoft, Redmond, United States of America).

### **Stimulus Materials and Task Design**

Participants were comfortably seated in a dimly lit electrically shielded recording chamber while performing a delayed match-to-sample task with an interleaved perceptual attention task (Fig. 1). The high-priority perceptual task required speeded button presses, and delayed responses were given in the memory task at the end of retention. Spatial attributes were relevant in both tasks, because subjects were asked to memorize a retrospectively cued location while attending to a prospectively cued location. Predictive retro-cues (memory task) and pre-cues (perceptual task) were simultaneously presented and pointed either in the same direction (compatible) or in the opposite directions (incompatible). Each cue indicated whether the left or right hand was relevant in the respective task. The memory task was to compare the retrospectively cued sample's location with the location of the subsequent test stimulus. In the perceptual attention task, participants were asked to detect transient irregularities in the prospectively cued vibrotactile stream.

The experimental procedure is shown in Figure 1: A trial started with bilateral presentation of tactile sample stimuli. Stimulus onset asynchrony (SOA) between samples and cues ranged between 290 and 390 ms (average 340 ms). Combined visual cues were shown for 600 ms and subsequently replaced by the fixation cross. The SOA between cues and vibrotactile streams was set to 690 ms. Streams had a duration of 3500 ms, with events inserted at 3 latencies (500, 1500, or 2500 ms relative to stream onset). A test stimulus was delivered to the retrospectively cued hand 620 ms after the offset of the vibrotactile streams. The SOA between the onset of vibrotactile streams and test equaled 4120 ms. A question mark shown on the monitor prompted for vocal responses with respect to the memory task during the 2600-ms period after test presentation. After that period, the next trial started with a slight time jitter between 0 and 100 ms. The experiment consisted of 440 trials, divided into 10 blocks of 5 min and 30 s. Feedback about average hit and correct rejection rates was given after each block. Prior to recordings, training sessions were conducted until stable accuracy was reached. Subjects trained both tasks separately before a session was performed under dual-task conditions.

### **Cue Stimuli**

The combined visual cues consisted of a retro- and pre-cue and were simultaneously presented for 600 ms on a monitor in front of the participants at viewing distance of 140 cm. The monitor's background color was set to black. Retro- and pre-cue consisted of a green and red arrowhead, respectively, with the retro-cue located above the pre-cue (Fig. 1). The letter "V" tilted by 90° or 270° served as an arrowhead with a width of 0.82° and 0.86° visual angle. Both arrowheads were horizontally centered in the middle of the screen (identical *x*-coordinate), while *y*-coordinates differed by 1.02° visual angle. Arrowhead borders were separated by 0.16° visual angle on the vertical axis. Directions of the retro- and pre-cue were independently randomized and pointed to the left (50%) or right side (50%). Thus, combined cues were either spatially compatible (same side, 50%) or incompatible (different sides, 50%).

### **Perceptual Attention Task**

Participants were instructed to detect transient irregularities (events) in the vibrotactile stream at the prospectively cued hand. Streams consisted of 3500 ms long amplitude-modulated waveforms with a carrier frequency of 100 Hz and an intensity of 0.9 N. To obtain separable SSSEPs, the modulating frequencies were set to 18 and 22 Hz for the left and right streams, respectively. In an interview after recordings, participants did not report systematic differences in the percepts elicited by the physically differing streams. Events consisted of a change of the carrier frequency to 70 Hz for 200 ms. Events were presented during consecutive "time windows" with fixed latencies of 500, 1500,

and 2500 ms relative to stream onset. For a particular time window, events were embedded into the attended (33%), ignored (33%), or both streams (33%). For each trial, we constrained the number of events to a maximum of 2, separated by an empty time window, because the requirement to perform responses in quick succession might lead to omission errors in subsequent time bins. The probability that a particular time window remained empty (no event in any stream) equaled 67%. In total, 432 events were presented during 440 trials, roughly corresponding to an average of one event per trial. Subjects were instructed to perform speeded responses to any event detected in the attended stream while ignoring the other side. Responses were given with the foot corresponding to the prospectively cued hand. The occurrence of events was balanced for all combinations of the experimental parameters time window (early, intermediate, and late) and "event location" (attended, bilateral, and ignored).

### **Memory Task**

Tactile sample and test stimuli consisted of single 5-ms pulses with an intensity of 0.37 N. Sample stimuli were simultaneously applied to the left and right hands. Each sample pulse was separately randomized to 1 location (finger) of the respective hand. The locations of sample stimuli were balanced across fingers (i.e. middle, ring, and small fingers) throughout the experimental trials. The test stimulus was presented to the retrospectively cued hand at a memorized (50%) or non-memorized location (50%). The locations of distracter test stimuli were statistically balanced across experimental conditions, since these events were randomized to 1 of the 2 nonmemorized fingers in each trial. Participants were instructed to decide whether the test had been delivered to the same location as the retrospectively cued sample stimulus.

### **Data Recording**

#### *Acquisition of Behavioral Responses*

In the perceptual task, participants used foot buttons to respond to transient changes in frequency (events) in the vibrotactile stream at the prospectively cued hand. Any event in the attended stream was defined as target, irrespective of whether an additional event occurred at the other hand. Therefore, unilateral events in the attended stream (33%) and bilateral events (33%) required a response, but not unilateral events in the ignored stream (33%). Participants were asked to respond with the foot anatomically corresponding to the prospectively cued hand. Such reactions were defined as "valid", while button presses with the other foot were considered as "invalid" responses. The first button press between 200 and 1200 ms after event onset was taken as response to this particular event. We averaged behavioral measures across hands, because preliminary analyses did not reveal significant differences dependent on the direction of the pre-cue (left and right).

As to the memory task, participants were prompted for the vocal response after the end of the retention delay. Speech signals were recorded by a microphone and submitted to voice-key routines written in MATLAB. The automatic classification of responses was performed on runtime and manually checked again offline. "Yes" and "no" responses were associated with the vowels "a" and "i", respectively. A hit was defined as "yes" response, provided that the test stimulus had been presented to the memorized location. A correct rejection was defined as "no" response, provided that the test stimulus had been delivered to a nonmemorized location.

#### *Recording of Electrophysiological Data and Treatment of Artifacts*

Brain activity was recorded at a sampling rate of 256 Hz from 64 Ag/AgCl electrodes, mounted in an elastic cap, using an ActiveTwo amplifier system (BioSemi, Amsterdam, The Netherlands). Electrode layout was in accordance with the extended international 10–20 system. During recordings, all scalp channels were referenced to an electrode next to POz. A bipolar outer canthus montage (horizontal electrooculogram) monitored lateral eye movements. A montage below and above the right eye (vertical electrooculogram) recorded vertical eye

movements and blinks. Data preprocessing was performed offline with the help of the EEGLab toolbox (Delorme and Makeig 2004) and custom written MATLAB routines. The continuous electroencephalography (EEG) data were bandpass filtered (0.5–30 Hz, Kaiser-windowed finite impulse response filter) and segmented into visual event-related potential (VEP), somatosensory event-related potential (SEP), and SSSEP epochs. SEP and SSSEP epochs. SEP and VEP epochs began 100 ms prior to visual cues and tactile stimuli (test stimuli, events in vibrotactile streams) and were corrected for a 100-ms pre-stimulus baseline. Relative to stimulus onset, VEP and SEP epochs extended for 800 and 500 ms, respectively. Vibrotactile streams were segmented into 1000-ms long SSSEP epochs, beginning at 500, 1500, and 2500 ms relative to stream onset. Linear trends were removed from SSSEP epochs.

Prior to artifact correction procedures, trials with horizontal eye movements >20  $\mu\text{V}$  (roughly corresponding to 1.5° of visual angle) were rejected. HEOG traces were individually screened for saccades and such epochs were discarded. “Independent component analysis” (Bell and Sejnowski 1995) performed blind source separation on EEG data. Independent components associated with eye blinks and vertical eye movements were identified by visual inspection (cf. Delorme et al. 2007; Mognon et al. 2011) and subtracted from individual EEG sets. Epochs exceeding a voltage threshold of  $\pm 150 \mu\text{V}$  were also discarded, while the remaining data entered “statistical control of artifacts in dense array EEG/MEG studies” (Junghöfer et al. 2000). SEP and VEP epochs were re-referenced to the arithmetic mean of both mastoids. Average reference was chosen for SSSEPs. Epoch rejection rates did not differ between experimental conditions for VEPs to cues (in average: 5.2%), SEPs to test stimuli (4.6%), SEPs to events in vibrotactile streams (6.2%), and SSSEPs to streams without events (9.0%).

### Statistical Analysis

Figure 2 summarizes the parameters (electrodes and time range) used to measure the VEP and SEP components. Electrodes and time ranges were defined according to the literature on the N2pc (Dell’Acqua et al. 2009; Kuo et al. 2009), early directing attention negativity (EDAN; van Velzen and Eimer 2003; Praamstra and Kourtis 2010), ADAN (Eimer et al. 2003, 2004), LDAP (Hopf and Mangun 2000; Eimer et al. 2003) of the VEP, and the somatosensory N140 (Eimer

et al. 2004; Forster and Eimer 2005) and LPC (Desmedt and Debecker 1979; Polich 2007) of the SEP. Note the different latency ranges for the LPC to test stimuli (memory task) versus events in ongoing steady-state stimulation (perceptual task); embedding events in an ongoing stimulation can reduce their saliency and thereby lead to temporally smeared out and delayed components.

VEPs and SEPs were obtained from recording clusters consisting of 3 averaged electrodes (Fig. 2); SSSEPs were acquired from a single electrode (see section Perceptual Attention Task). VEPs, SEPs, and SSSEPs were averaged across hands, because preliminary analyses of electrophysiological and behavioral data exhibited consistent patterns of results for the left and right hands. Amplitudes were averaged throughout the latency range of particular components (Fig. 2) and submitted to repeated-measures analysis of variances (ANOVAs). Greenhouse–Geisser adjustments were applied whenever necessary. Error bars (EBs) in figures reflect the error terms associated with particular effects of interest, independent of between-subject variance (cf. Loftus and Masson 1994; Jarmasz and Hollands 2009). Here, conditional means with nonoverlapping EBs represent a significant effect ( $P < 0.05$ ) of the experimental manipulation specified in the respective figure caption. EBs in VEP/SEP graphs (gray shading) are for illustrative purpose and were not Bonferroni corrected.

### Cue-Related Activity

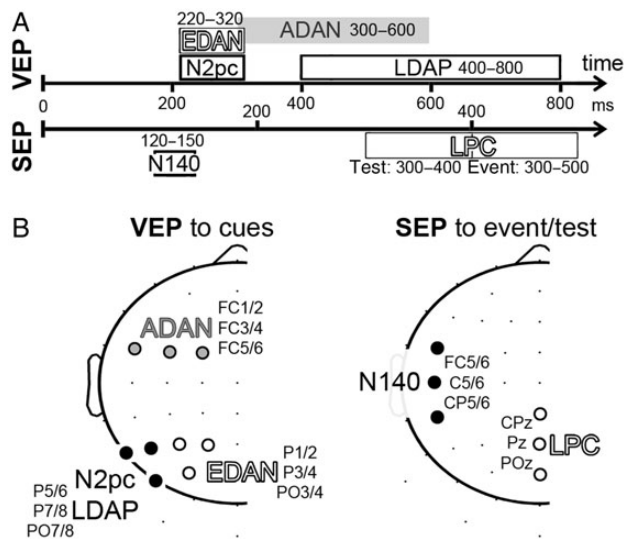
VEPs to the combined cues were acquired at anterior and posterior scalp regions contralateral and ipsilateral to the direction of the pre-cue. The difference of contralateral minus ipsilateral VEP amplitudes entered statistical assessment. Separate *t*-tests against zero for the compatible and incompatible cue condition examined the statistical robustness of lateralized components (N2pc, EDAN, ADAN, and LDAP; an EDAN emerged unexpectedly in the incompatible cue condition. In line with prior evidence [Praamstra and Kourtis 2010], the EDAN mirrored prospective attention shifts [pre-cue direction], overlapped with N2pc latency, but manifested at more parietal electrodes than the N2pc; Fig. 3). Paired *t*-tests contrasted difference values in compatible versus incompatible cue trials to assess whether the size of lateralized effects differed between the conditions of “cue compatibility.” A follow-up test compared N2pc and EDAN using a 2-way ANOVA with the factors cue compatibility and “component” (N2pc and EDAN).

### Perceptual Attention Task

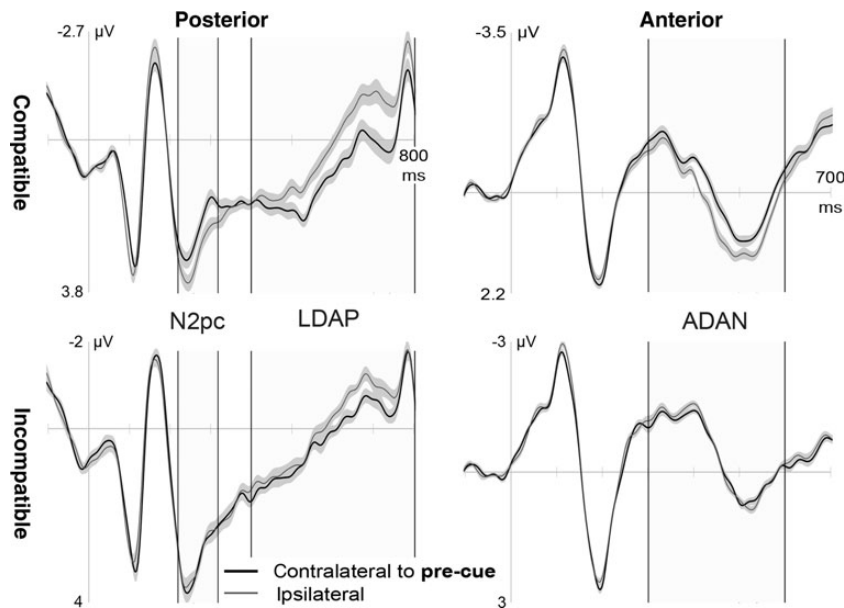
We analyzed electrophysiological and behavioral responses to tactile stimuli involved in the perceptual attention task. The epochs of vibrotactile streams without transient events and behavioral responses entered the analysis of SSSEP amplitudes. Epochs with transient events were subjected to the analysis of the LPC.

To examine SSSEP amplitudes, epochs were averaged across the trials of a particular experimental condition and subsequently transformed to the frequency domain by means of the fast Fourier algorithm. The modulator frequency of the left and right vibrotactile streams was set to 18 and 22 Hz, respectively. SSSEP amplitudes driven at these frequencies were calculated for a single electrode contralateral to stimulation and after normalization, averaged across both hands (i.e. frequencies). Electrodes FC3 (22 Hz) and FC2 (18 Hz) were chosen for statistical tests, as these exhibited maximal SSSEP amplitudes when averaged across participants and experimental conditions. The normalization procedure of SSSEP amplitudes was separately performed for each frequency and participant and is for a given frequency as follows: Amplitudes measured in particular experimental conditions were divided by the average amplitude across all conditions (e.g. Andersen et al. 2011). After normalization, the influence of an experimental manipulation is quantified by a value deviating from 1. Normalized amplitudes were calculated for the left (18 Hz) and right streams (22 Hz), averaged across hands, and submitted to a 2-way ANOVA with the factors of cue compatibility (compatible and incompatible) and “attended stream” (attend and ignore).

The LPC to transient events in ongoing stimulation was measured at a single posterior electrode cluster (Fig. 2). LPC amplitudes entered a 2-way ANOVA with the factors of cue compatibility (compatible and incompatible) and event location (attended, bilateral, and ignored).



**Figure 2.** (A) Time windows for the measurement of VEP (top) and SEP (bottom) components. Note the differing LPC time ranges for isolated test stimuli versus events in ongoing vibrotactile stimulation. (B) Electrode selection for VEP (left) and SEP (right) components. Lateralized VEP components were measured at symmetric recording clusters contra- and ipsilateral to the pre-cue direction (only 1 hemisphere is shown here). The N140 of the SEP was acquired contra- and ipsilateral to stimulation. The LPC of the SEP was measured at a single nonlateralized recording cluster.



**Figure 3.** Grand mean VEPs to compatible and incompatible cues are shown in separate rows. VEPs were measured at lateral posterior (left) and anterior (right) scalp regions, contralateral (black line) and ipsilateral (gray) to the pre-cue direction. EBs (shaded) were separately estimated for compatible and incompatible cues and are based on the effect of electrode cluster. At a given time point, nonoverlapping EBs reflect the presence of lateralized activity.

To examine the interaction between these factors, we calculated LPC difference values of compatible minus incompatible trials. Difference values were separately tested against zero for the factor levels of event location. Kendall's  $\tau$  was computed to test the LPC difference values for a monotonic trend across events at unilateral attended, bilateral, and unilateral ignored locations.

Behavioral performance of target detection (speed and accuracy) entered separate 2-way ANOVAs with the factors of cue compatibility (compatible and incompatible) and time window (early, intermediate, and late). The factor levels of time window correspond to the latency of event presentation. The analysis of unilateral events examined only valid responses (see section Acquisition of Behavioral Responses): Responses to "attended" and "ignored" events were defined as hits and false alarms, respectively. The analysis of bilateral events included valid and invalid responses that were defined as hits and false alarms, respectively. Reaction times of valid responses to target events (unilateral attended and bilateral) were submitted to further ANOVAs with equivalent design as described above.

#### Memory Task

The somatosensory N140 component evoked by test stimuli was acquired at scalp regions contralateral and ipsilateral to stimulation (Fig. 2). N140 amplitudes entered a 2-way ANOVA, comprising the factors of cue compatibility (compatible and incompatible) and "electrode cluster" (contralateral and ipsilateral). The LPC was measured a single electrode cluster and subjected to a paired *t*-test for cue compatibility (compatible and incompatible).

Accuracy measures, such as hit and correct rejection rates, were assessed by separate 2-way ANOVAs with the factors of cue compatibility (compatible and incompatible) and "cued hand" (direction of retro-cue: Left vs. right).

## Results

### Cue-Related Activity

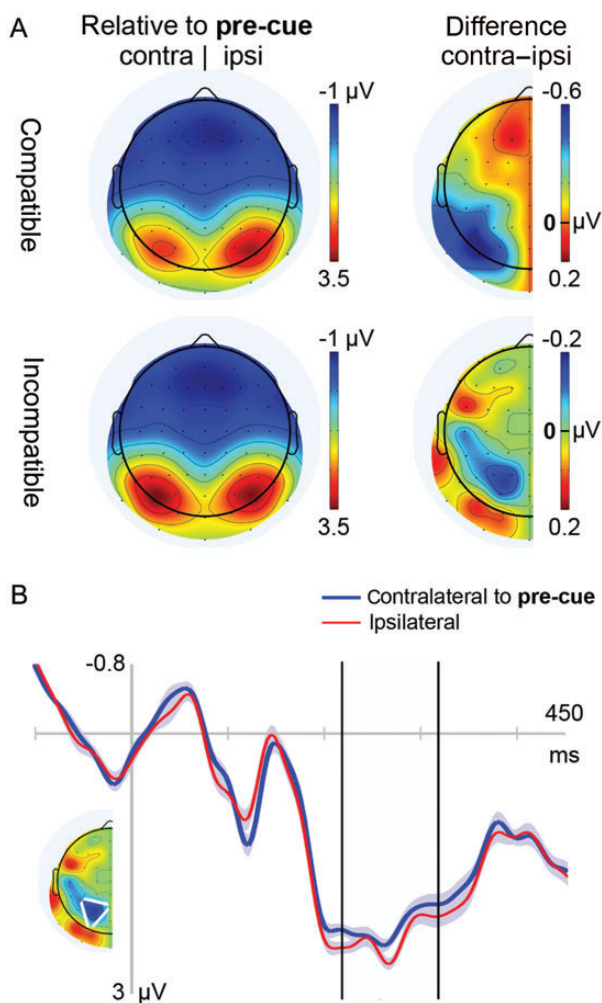
The combined visual cues elicited 1 anterior (ADAN) and 3 posterior (N2pc, EDAN, and LDAP) lateralized components; compare Figures 2, 3, and 4. Both N2pc and EDAN occurred in the same time range (220–320 ms post-cue) and were

measured at nearby, but not identical electrodes (cf. Praamstra and Kourtis 2010). These components were followed by the fronto-central ADAN (300–600 ms) and the posterior LDAP (400–800 ms), which were measured at the same electrodes as the N2pc.

The magnitude of lateralized activity is quantified by difference values of amplitudes recorded contra- minus ipsilateral to the direction of the pre-cue. Most importantly, a paired *t*-test assessed whether the magnitude of lateralized effects differed between the cue conditions. Furthermore, separate *t*-tests against zero for compatible and incompatible trials examined the statistical robustness of particular lateralized components. Difference values deviating from zero indicate the presence of a lateralized effect, irrespective of its polarity. Lateralized components with reversed polarity would mirror the opposite direction of the pre-cue.

For the compatible condition, the polarity of these components consistently reflected the side indicated by both cues (N2pc:  $t_{(17)} = -4.258$ ,  $P < 10^{-3}$ ; EDAN:  $t_{(17)} = -3.897$ ,  $P = 0.001$ ; ADAN:  $t_{(17)} = -4.708$ ,  $P < 10^{-3}$ ; LDAP:  $t_{(17)} = 4.453$ ,  $P < 10^{-3}$ ). The magnitude of all 4 lateralized components was reduced in the incompatible condition, relative to compatible cue trials (N2pc:  $t_{(17)} = -3.998$ ,  $P < 10^{-3}$ ; EDAN:  $t_{(17)} = -2.444$ ,  $P = 0.026$ ; ADAN:  $t_{(17)} = -4.629$ ,  $P < 10^{-3}$ ; LDAP:  $t_{(17)} = 3.363$ ,  $P = 0.004$ ). Only the EDAN and LDAP still reflected the direction of the pre-cue (EDAN:  $t_{(17)} = -2.480$ ,  $P = 0.024$ ; LDAP:  $t_{(17)} = 2.603$ ,  $P = 0.019$ ), while the other lateralized components were entirely attenuated, that is, not significantly different from zero (N2pc:  $t_{(17)} = 0.238$ ,  $P = 0.814$ ; ADAN:  $t_{(17)} = 0.594$ ,  $P = 0.560$ ).

The pre-cue differed from the retro-cue in terms of color and location, since a red pre-cue was presented on the monitor below a green retro-cue. To explore whether these physical parameters (color, location) were the cause of the EDAN modulation, we recorded 3 additional participants with reversed cueing instructions. For these subjects, a green pre-



**Figure 4.** (A) Grand mean isocontour voltage maps and difference maps in the N2pc latency range, in response to compatible and incompatible cue configurations. Note varying scales of difference maps. (B) Grand mean VEPs to incompatible cues, obtained contralateral (black line) and ipsilateral (gray line) to the pre-cue direction at posterior scalp regions (white triangle). The EDAN was measured during the N2pc time range (black boundaries). EBs based on the effect of electrode cluster.

cue was presented above a red retro-cue. Throughout all of these participants, the EDAN mirrored pre-cue direction in incompatible and compatible cue trials.

The apparent dissociation of N2pc and EDAN (Fig. 4) was tested with a design comprising the additional factor of component (N2pc and EDAN). The impression that these components exhibited differential patterns of modulation across the conditions of cue compatibility was statistically substantiated by a component  $\times$  cue compatibility interaction ( $F_{1,17} = 13.131$ ,  $P = 0.002$ ). There was no significant difference between the size of N2pc and EDAN when the levels of cue compatibility were not taken into account (component:  $F_{1,17} = 0.182$ ,  $P > 0.1$ ). As already stated above, the magnitude of lateralized activity in the N2pc–EDAN time range was reduced in the incompatible cue condition, relative to compatible cues (cue compatibility:  $F_{1,17} = 14.109$ ,  $P = 0.002$ ).

### Perceptual Task

Behavioral performance in the attention task was impaired in the incompatible cue condition when compared with the

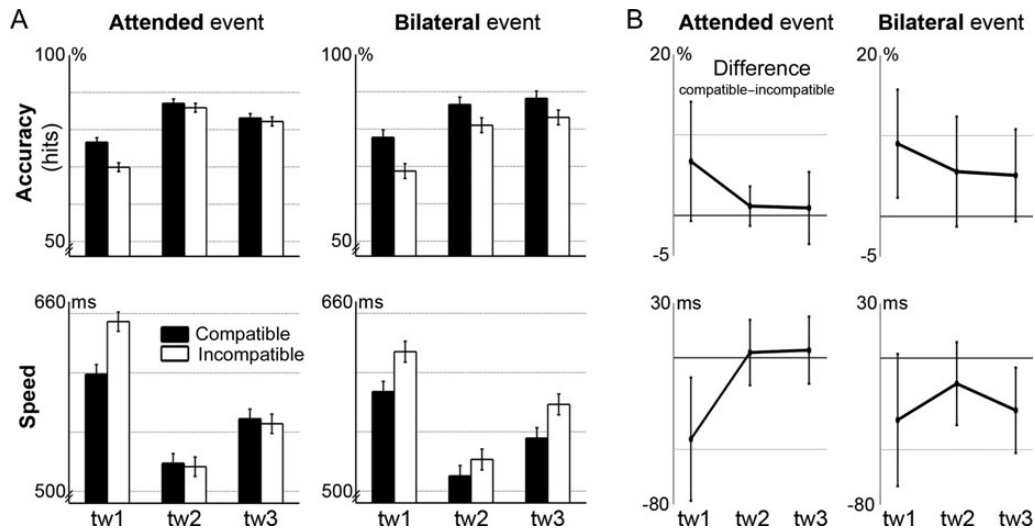
compatible condition. Unilateral attended and bilateral events were targets and required speeded foot button presses. The analysis of unilateral events was restricted to valid responses, that is, button press at the prospectively cued body side. Valid and also invalid responses entered the analysis of bilateral events.

As to unilateral events, incompatible cues reduced the accuracy of target detection in a sustained manner, independent of event latency, and caused a transient delay of reaction times for early events. Hit rates were lower in the incompatible condition (cue compatibility:  $F_{1,17} = 6.692$ ,  $P = 0.019$ ) and this effect generalized across the latencies of event presentation, since there was no significant interaction of cue compatibility  $\times$  time window ( $P > 0.1$ ). Reaction times mirrored such an interaction (cue compatibility  $\times$  time window:  $F_{2,34} = 6.938$ ,  $P = 0.003$ ), but not a main effect of cue compatibility ( $P > 0.1$ ). As shown in Figure 5, the slowing of reaction times due to incompatible cues was restricted to events that were presented in the “early” time bin (time window 1:  $t_{(17)} = -2.785$ ,  $P = 0.013$ ). No differences were found for subsequent bins (time window 2:  $t_{(17)} = 0.344$ ,  $P > 0.1$ ; time window 3:  $t_{(17)} = 0.485$ ,  $P > 0.1$ ). Less importantly, performance depended on the time window of event presentation (hit rates:  $F_{1,41,24,02} = 23.076$ ,  $P < 10^{-6}$ ; reaction times:  $F_{1,38,23,41} = 29.150$ ,  $P < 10^{-7}$ ); the least accurate and slowest responses were associated with early events. False alarm rates, that is, valid responses to unilateral events in the ignored stream, were not sensitive to the experimental manipulations (all  $P > 0.1$ , average: Compatible: 8.72% and incompatible: 8.22%).

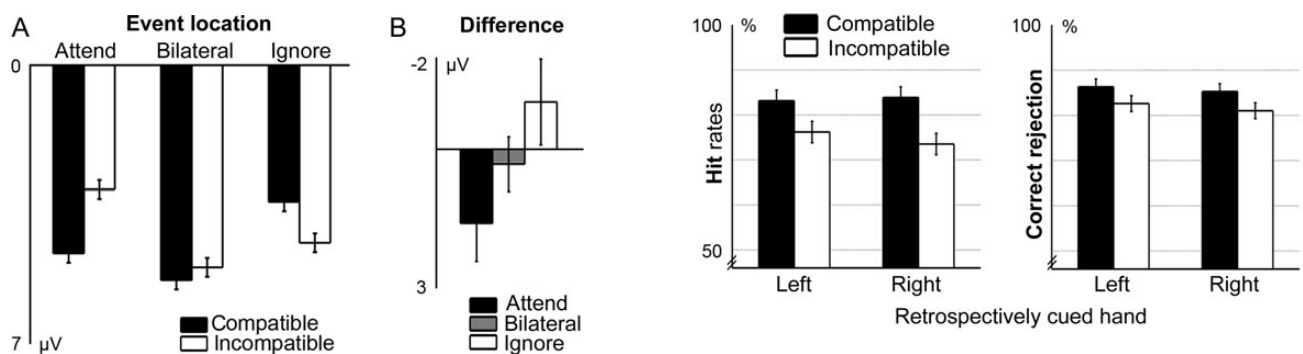
The detection of bilateral targets was subject to sustained performance decrements in the incompatible, relative to the compatible condition. Incompatible cues reduced behavioral performance (hit rates:  $F_{1,17} = 12.415$ ,  $P = 0.003$ ; reaction times:  $F_{1,17} = 9.279$ ,  $P = 0.007$ ) in the absence of significant cue compatibility  $\times$  time window interactions (all  $P > 0.1$ ). Furthermore, the factor of time window influenced performance (hit rates:  $F_{2,34} = 14.260$ ,  $P < 10^{-4}$ ; reaction times:  $F_{1,20,20,47} = 18.643$ ,  $P < 10^{-5}$ ) in a similar pattern as described above for unilateral events. False alarm rates, corresponding to invalid responses (cf. section Acquisition of Behavioral Responses), were generally low and did not differ between conditions ( $P > 0.1$ , compatible: 0.54% and incompatible: 1.16%). Since the occurrence of invalid responses did not reflect whether the retro-cue pointed in the same or opposite direction of the pre-cue, performance decrements due to incompatible cues were not correlated with failures to respond with the appropriate effector.

SSSEP amplitudes to vibrotactile streams without events were not sensitive to the experimental manipulations: Amplitudes did not differ between the prospectively cued and uncued stream (attended stream:  $F_{1,17} = 1.213$ ,  $P > 0.1$ ). There was no cue compatibility main effect ( $F_{1,17} = 0.301$ ,  $P > 0.1$ ) and no interaction between the manipulations (attended stream  $\times$  cue compatibility:  $F_{1,17} = 0.164$ ,  $P > 0.1$ ). A follow-up analysis extended the design by the factor of “attended frequency” contrasting the prospectively cued streams that were modulated at 18 (left hand) and 22 Hz (right hand), but did also not reveal significant effects or interactions (all  $P > 0.1$ ).

Participants were asked to detect target events in the prospectively cued vibrotactile stream. Unilateral attended and bilateral events matched the location indicated by the pre-cue and, hence, were targets requiring the behavioral response.

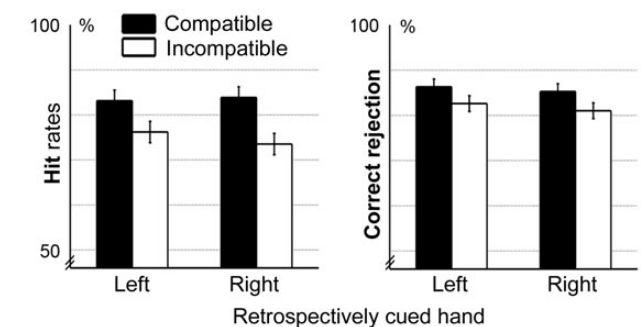


**Figure 5.** Perceptual task performance. (A) Hit rates (upper row) and reaction times (lower row) to events in vibrotactile streams that required immediate responses. Such events were either inserted into the attended stream only or simultaneously presented to both hands (bilateral). Black and white bars represent accuracy measures for compatible and incompatible cue trials, respectively, as function of the time window of event presentation (tw: 500, 1500, or 2500 ms relative to stream onset). EBs designate the main effect of cue compatibility, obtained from separate ANOVAs for a specific behavioral measure (accuracy and speed) and event location (unilateral attended and bilateral). (B) Difference values were calculated by subtracting behavioral measures of the compatible minus incompatible cue condition. EBs reflect the influence of event time window on difference values (i.e. the cue compatibility effect) and were estimated by separate statistical tests for a particular measure and event location.



**Figure 6.** LPC to events in vibrotactile streams. (A) Grand mean amplitudes of the LPC, elicited by transient events in ongoing vibrotactile streams. LPC amplitudes in the compatible (black bars) and incompatible (white bars) cue condition are grouped by event location: Events were inserted in the attended or ignored stream, or in both streams. EBs based on the main effect of cue compatibility. (B) LPC modulations due to cue compatibility in terms of difference values of compatible minus incompatible cue trials. The influence of event location on LPC modulations is illustrated for unilateral attended (black), bilateral (gray), and unilateral ignored events (white). EBs based on separate tests of LPC difference values against zero for the factor levels of event location.

Unilateral ignored events served as distracters. The LPC (300–500 ms) evoked by events in incompatible cue trials did not significantly differ from LPC amplitudes elicited in the compatible condition (cue compatibility:  $F_{1,17} = 1.761$ ,  $P > 0.1$ ). The location of event presentation influenced the LPC (event location:  $F_{2,34} = 14.416$ ,  $P < 10^{-4}$ ), whose amplitudes were largest for bilateral events (compare Fig. 6). LPC amplitudes revealed an interaction between cue compatibility and event location ( $F_{2,34} = 12.344$ ,  $P = 10^{-4}$ ). We then subtracted LPC amplitudes in compatible minus incompatible cue trials to further investigate the interaction. The calculated difference values exhibited a clear monotonic trend across events at (unilateral) attended, bilateral, and (unilateral) ignored

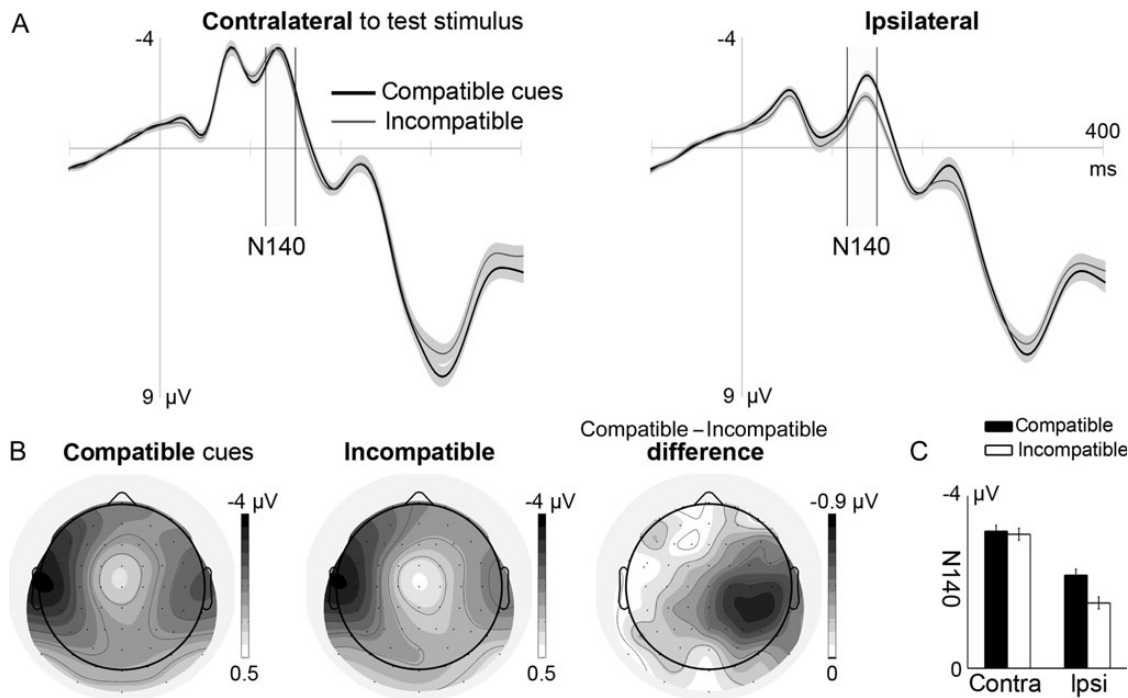


**Figure 7.** Memory task performance in terms of average hit (left) and correct rejection rates (right), dependent on retro-cue direction. Performance in compatible and incompatible cue trials are represented by black and white bars, respectively. EBs are based on the main effect of cue compatibility, separately estimated for hit and correct rejection rates.

locations ( $\tau = -0.533$ ,  $P < 10^{-6}$ ; Fig. 6). LPC difference values were positive for targets, although this effect was statistically significant only for unilateral attended ( $t_{(17)} = 4.054$ ,  $P < 10^{-3}$ ), but not bilateral events ( $t_{(17)} = 1.146$ ,  $P > 0.1$ ). Distracters led to negative LPC difference values ( $t_{(17)} = -2.325$ ,  $P = 0.033$ ). Notably, positive difference values indicate a reduced LPC due to incompatible cues relative to the compatible condition, while negative difference values represent LPC enhancement. The location of event presentation systematically altered the influence of the cue compatibility effect on LPC amplitudes, dependent on how well spatial attributes of events matched with the prospectively cued location.

### Memory Task

The disruption of attention-based rehearsal by means of attention shifts to nonmemorized locations was expected to impair memory performance. Hit rates and correct rejections were



**Figure 8.** (A) Grand mean SEPs to test stimuli in compatible (black line) and incompatible cue trials (gray line). EBs based on the cue compatibility effect, separately estimated for contralateral and ipsilateral recordings. (B) Grand mean voltage maps in the N140 time range for the compatible and incompatible cue conditions. The difference map represents subtracted voltage maps of compatible minus incompatible cue trials, illustrating the topographical extent of N140 modulations due to cue compatibility. The arrangement of data in voltage and difference maps corresponds to stimulation of the right hand. (C) Mean N140 amplitudes as function of the design factors of cue compatibility and electrode cluster. EBs reflect the main effect of cue compatibility.

lower for trials with incompatible cues (cue compatibility: Hit rate:  $F_{1,17} = 14.800$ ,  $P = 0.001$ ; correct rejections:  $F_{1,17} = 5.865$ ,  $P = 0.027$ ; Fig. 7). Neither hit rates nor correct rejections depended upon whether the left or right hand was cued (cued hand: Hit rate:  $F_{1,17} = 1.165$ ,  $P > 0.1$ ; correct rejections:  $F_{1,17} = 0.341$ ,  $P > 0.1$ ). There were no significant interactions between cue compatibility and cued hand in hit rates as well as correct rejections (all  $P > 0.1$ ).

The somatosensory N140 (120–150 ms) to test stimuli was reduced in the incompatible condition when compared with compatible cue trials (cue compatibility:  $F_{1,17} = 7.561$ ,  $P = 0.014$ ; Fig. 8). This effect was strongly lateralized to scalp regions ipsilateral to stimulation (cue compatibility  $\times$  cluster:  $F_{1,17} = 14.129$ ,  $P = 0.002$ ). The LPC (300–400 ms) showed a similar pattern: Amplitudes were reduced in the incompatible condition, relative to compatible cue trials (cue compatibility:  $t_{(17)} = 2.534$ ,  $P = 0.021$ ).

## Discussion

There is a conceptual redundancy between the construct of an executive system supervising STM operations and selective attention (Baddeley 2003; Zimmer 2008; Gazzaley 2011; Gazzaley and Nobre 2012). We conducted a tactile dual-task study in which participants were asked to memorize a retrospectively cued location while simultaneously attending to a prospectively cued location. The crucial comparison was whether the locations relevant in both tasks were nearby (same hand and compatible cues) or far apart (opposite hands and incompatible cues). If spatial selection in STM and perception engages encapsulated—functionally

independent—neural systems, there should be no costs of incompatible directional instructions, relative to compatible cues. If spatial selection, however, is mediated by a unitary control system subservient to both memory and perception, incompatible cues should lead to interferences in behavioral performance and electrophysiological activity reflecting the division of spatial attention between both hands.

Our results substantiate a major claim of the attention-based rehearsal account, namely, the functional significance of spatial attention for the maintenance of spatial information in STM (reviewed by Awh et al. 2006). STM accuracy decreased when attention was withdrawn from memorized locations. We further observed a drop in perceptual task performance for incompatible cues. These bidirectional interdependencies between memory and perception suggest an intimate link between these domains rather than independently operating neural circuits (Pasternak and Greenlee 2005; Awh et al. 2006; Bengson and Mangun 2011; Gazzaley and Nobre 2012). Spatial selection in STM and perception relies on a common set of executive functions that are subject to capacity limitations (Baddeley 2003; Bengson and Mangun 2011).

### Functional Significance of Attention-Based Rehearsal

The current experiment resolves a standing controversy regarding whether spatial attention underlies optimal spatial STM performance (Awh and Jonides 2001; Awh et al. 2006). A series of visual studies reported attention shifts toward memorized locations during the retention period; this observation led to the conclusion that spatial attention mediates the maintenance of locations (Awh et al. 2000; Jha 2002). Alternatively, such spatial attention effects might represent an



epiphenomenon without causal relation to memory accuracy, as suggested by Belopolsky and Theeuwes (2009b) who reported results inconsistent with this view.

In the sense of touch, we previously showed that the memorization of locations causes spatial attention shifts that influence sensory encoding of subsequent peripheral events (Katus et al. 2012a). The current study substantiates a further assumption of the attention-based rehearsal account: The requirement to direct attention away from memorized locations impairs memory accuracy and influences the somatosensory N140 to test stimuli, a component sensitive to spatial attention (e.g. Forster and Eimer 2005) and conscious perception (Schubert et al. 2006). Such early effects in somatosensory areas converged with modulations of neural activity in downstream regions, as reflected by the LPC (Desmedt and Debecker 1979; Sambo and Forster 2011).

There are at least 3 lines of arguments that might explain why the present tactile study found a functional significance of attention-based rehearsal despite the mixed results of previous visual experiments (Awh et al. 2006; Belopolsky and Theeuwes 2009b). First, we sought to maximize the influence of prospective attention shifts on spatial STM. To reduce the amount of resources available to the memory task, participants were asked to prioritize the perceptual task. Secondly, spatial attributes were explicitly relevant in both tasks, which were not the case in some of the visual studies mentioned above (Belopolsky and Theeuwes 2009b). Thirdly, we used simultaneously presented predictive cues to trigger the endogenous shifts of retrospective and prospective attention to the same or opposite spatial directions. Overall, the present study demonstrates that spatially specific biasing of mnemonic information represents an adaptive strategy to optimize the accuracy of spatial STM (Awh and Jonides 2001; Awh et al. 2006).

### ***Control Processes Common to STM and Perception***

Common mechanisms mediate spatial selection in internal and external stimulus representations (Awh and Jonides 2001; Curtis and D'Esposito 2003; Griffin and Nobre 2003; Awh et al. 2006; Belopolsky and Theeuwes 2009a, 2011; Theeuwes et al. 2009). Numerous lesion and imaging studies have reported an engagement of overlapping substrates in memory and perception (Awh and Jonides 2001; Curtis and D'Esposito 2003; Naghavi and Nyberg 2005; Pasternak and Greenlee 2005; Müller and Knight 2006; Sörös et al. 2007). In addition to the anatomical overlap, we provide evidence that spatially specific biasing of STM relies on the same capacity-limited functions that are involved in perception. Incompatible cues led to a division of spatial attention between both hands, as revealed by behavioral performance and physiological measures originating in anterior (ADAN), fronto-parietal (N140), and posterior (e.g. LDAP) neural networks.

Selective maintenance of locations in tactile STM influences the processing of external events in a spatially specific manner (Katus et al. 2012a). Retro-cues that pointed in the opposite direction of pre-cues reduced behavioral performance in the prioritized, perceptual task. Participants responded slower and less accurately to events presented at perceptually attended locations in incompatible cue trials, relative to the compatible condition. We outlined above that the accuracy of spatial STM depended on whether the

perceptually attended location was a part of the memorized hand. Taken together, these results point toward a close and bidirectional relation between spatial selection in external and internal stimulus representations. Since performance in either task depended on the relevant location in the other task, we conclude that the spatial selection of external events is of functional significance for spatial selection in STM and vice versa, which strongly suggests that both domains rely on shared executive processes (Awh and Jonides 2001; Naghavi and Nyberg 2005; Awh et al. 2006; Theeuwes et al. 2009; Gazzaley and Nobre 2012).

Is the incompatible cue interference truly an effect of spatial attention? One might alternatively argue that the observed interference between both tasks was related to the similarity of low-level codes. More specifically, both tasks involved responses that depended upon spatial stimulus attributes. The question here is whether interference between the perceptual and STM tasks reflects shared “codes” for locations or shared “control functions” for spatial attention. Interference caused by common spatial codes should be high for similar spatial attributes. Accordingly, interference should be greater when memorized and perceptually attended stimuli are presented at nearby locations, that is, the compatible cue condition. Contrary to that, interference emerged in the incompatible cue condition where memorized and perceptually attended stimuli were located at different hands, and thus, had dissimilar spatial attributes. Common spatial codes per se cannot explain our results without taking spatial attention into account. Clear evidence that compatible and incompatible cues correspond to conditions of focused and divided spatial attention, respectively, comes from the analysis of late cue-related neural responses described in the next section.

Selection in internal and external stimulus representations is mediated by a unitary control system that governs conjoint activity of distributed anterior and posterior neural networks. Late lateralized components (ADAN and LDAP) are equally sensitive to retrospective (Griffin and Nobre 2003; Katus et al. 2012a, 2012b) and prospective shifts of spatial attention (Eimer and van Velzen 2002; van Velzen et al. 2002; Eimer et al. 2003; Griffin and Nobre 2003; van Velzen and Eimer 2003; Eimer et al. 2004; Forster et al. 2009). The reduced size of these components in the incompatible cue condition indicates a suboptimal guidance of prospective attention shifts due to the selection of spatially incongruent information in tactile STM. Selection in mnemonic and external representations of sensory signals involves equivalent control functions, indexed by late lateralized components, whose interpretation as markers of preparatory attention is therefore misleading (van Velzen et al. 2002, in opposition to, e.g. Eimer et al. 2004; Seiss et al. 2009; Murray et al. 2011).

### ***Processes Specific to Prospective Attention***

Selection in STM and perception involves equivalent functions that operate at a relatively early stage in the guidance of attention shifts. The N2pc component—an established marker of perceptual attention (Luck and Hillyard 1994a, 1994b)—is presumably the earliest electrophysiological measure sensitive to selection in mnemonic representations (Dell'Acqua et al. 2009; Kuo et al. 2009; Katus et al. 2012a, 2012b). However, a further lateralized component in the same time range does not apparently exhibit such functional overlap of STM and perception. The EDAN may reflect a neural process specific to

the initiation of prospective attention shifts (Hopf and Mangun 2000; Jongen et al. 2007; Praamstra and Kourtis 2010).

The EDAN is not the N2pc. These early lateralized components are evoked by visual events and have comparable topographical and temporal distributions. Such similarities led to the proposal that the EDAN is not an existing component, but an “N2pc in disguise” (van Velzen and Eimer 2003). The EDAN typically emerges in experiments using lateralized cue stimuli, such as arrow cues (Jongen et al. 2007). It was therefore argued that spatially specific encoding of asymmetric visual cues triggered the N2pc that was then erroneously interpreted as EDAN in prior experiments (van Velzen and Eimer 2003). Consistent with that assertion, the compatible cue EDAN here was not distinguishable from the simultaneously present N2pc. This confound was resolved in the incompatible condition. The EDAN still mirrored the prospectively cued location despite complete attenuation of the occipito-temporal N2pc (cf. Praamstra and Kourtis 2010). The dissociation of these lateralized effects rules out the interpretation that the EDAN is the N2pc in disguise and settles the debate regarding the proposed identity of these components (van Velzen and Eimer 2003, in opposition to Praamstra and Kourtis 2010).

### ***Interactions of Memory and Perception Within and Beyond Somatosensory Regions***

Top-down influences from modality-unspecific regions regulate neural activity in modality-specific regions, such as secondary (SII), and, to a lesser degree, primary (SI) somatosensory cortex (Johansen-Berg and Lloyd 2000; Sambo and Forster 2011). Here, incompatible cues modulated electrophysiological measures reflecting supramodal attention (ADAN and LDAP; Eimer and van Velzen 2002; van Velzen et al. 2002; Eimer et al. 2003; Seiss et al. 2007), somatosensory encoding (N140; Sambo and Forster 2011), and subsequent memory processing (LPC; Polich 2007). Neural operations within and beyond the somatosensory system were hence subject to interference when incompatible cues triggered attention shifts in opposite directions. In particular, the impaired generation of supramodal biasing signals points to the functional overlap of STM and perception at a high level in the hierarchy of attentional control.

The influence of cue compatibility on the N140 component represents an interaction of spatial selection in STM and perception occurring within the somatosensory system (Eimer et al. 2004; Sambo and Forster 2011; Hu et al. 2012), since the N140 is generated in fronto-parietal regions that include secondary somatosensory cortex (SII; Allison et al. 1992; García-Larrea et al. 1995; Frot and Mauguière 1999; Waberski et al. 2002). Although it is well known that the N140 is enhanced when a stimulated hand is attended relative to ignored (Josiasen et al. 1982; Michie et al. 1987; Eimer and Forster 2003; Forster and Eimer 2004, 2005; Zopf et al. 2004), the cue compatibility effect here is not trivial. Unlike in the mentioned studies, we did not compare the N140 elicited by stimuli at an attended versus ignored hand, because test stimuli were always presented to the retrospectively cued hand. The disruption of attention-based rehearsal by means of prospective attention shifts to nonmemorized locations attenuated the N140; this effect converged with a decrease in memory accuracy and a reduction of LPC amplitudes. An unresolved issue,

however, is why the attentional N140 modulation was confined to ipsilateral regions.

Influence from STM affects the decision whether an event in the sensory periphery is a target or a distracter. External events elicit the LPC that is thought to reflect cognitive operations such as memory processing (Polich 2007). LPC amplitudes are typically enhanced for targets, relative to distracters (Desmedt and Debecker 1979; Polich 2007; Sambo and Forster 2011). Compared with compatible cues, however, this relation was reversed in the incompatible condition where LPC amplitudes were reduced for targets and enhanced for distracters. The magnitude of interference caused by incompatible cues was quantized using LPC difference values that mirrored a monotonic trend across unilateral attended, bilateral, and unilateral ignored external events. Hence, the categorization of an external stimulus as target versus distracter depended on how well its spatial attributes matched those of a simultaneously memorized location. The interference from STM on the evaluation of external events at such late stage of neural processing is evidence for overlapping mechanisms of STM and perception downstream to the somatosensory system (Polich 2007; Sambo and Forster 2011).

The experimental manipulations did not affect the SSSEP with putative generators in SI (Giabbiconi et al. 2007). The absence of a spatial bias in earliest somatosensory areas along with the attention effect at late stage (LPC) might be consequence of a delayed spatial filter in the context of concurrently established cognitive load (Lavie 2005). While this interpretation remains speculative here, the LPC component and behavioral measures clearly showed that spatial STM hampers the processing of external events presented at nonmemorized locations.

### **Conclusion**

Participants were asked to memorize a retrospectively cued location while attending to a prospectively cued location. Interference emerged when memorized and attended locations were far apart (different hands) relative to nearby (same hand). First, the disruption of attention-based rehearsal impaired memory accuracy and affected somatosensory encoding, suggesting that spatial attention is a core element for the maintenance of spatial STM and a prerequisite for optimal memory accuracy (Awh and Jonides 2001; Awh et al. 2006). Secondly, costs of retro-cues that directed attention away from prospectively attended locations were evident in the prioritized perceptual task. Thirdly, the attenuation of lateralized activity due to incompatible cues converged with the pattern of results observed in the analysis of either task dependent of the other. Overall, we found bidirectional interactions between the neural systems mediating spatial selection in STM and perception (Awh et al. 2006; Gazzaley 2011; Gazzaley and Nobre 2012).

STM and perception are subject to capacity limitations (Bengson and Mangun 2011). The pattern of interference that we observed strongly suggests that both domains rely on the same resource, spatial attention, which was divided between the left and right hands in the incompatible cue condition. The costs of incompatible cues altered activity of distributed neural processes associated with multiple levels in the hierarchy of attentional control, up to supramodal systems. We conclude that spatial selection in memory and perception relies

on common control processes, pointing to the engagement of a unitary capacity-limited mechanism rather than domain-specific encapsulated modules. It should be noted, however, that we also observed an early neural process (EDAN) that might be specific to prospective shifts of spatial attention.

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