

Nonspatial Cueing of Tactile STM Causes Shift of Spatial Attention

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Abstract

■ The focus of attention can be flexibly altered in mnemonic representations of past sensory events. We investigated the neural mechanisms of selection in tactile STM by applying vibrotactile sample stimuli of different intensities to both hands, followed by a symmetrically shaped visual retro-cue. The retro-cue indicated whether the weak or strong sample was relevant for subsequent comparison with a single tactile test stimulus. Locations of tactile stimuli were randomized, and the required response did not depend upon the spatial relation between cued sample and test stimulus. Selection between spatially segregated items in

tactile STM was mirrored in lateralized activity following visual retro-cues (N2pc) and influenced encoding of task-irrelevant tactile probe stimuli (N140). Our findings support four major conclusions. First, retrospective selection results in transient shifts of spatial attention. Second, retrospective selection is functionally dissociable from attention-based rehearsal of locations. Third, selection mechanisms are linked across processing stages, as attention shifts in STM influence encoding of sensory signals. Fourth, selection in tactile STM recruits attentional control mechanisms that are, at least partially, supramodal. ■

INTRODUCTION

STM defines the capability to maintain and manipulate previously perceived information in mind. The content of STM is subject to attentional influences and similar to the perceptual domain; the focus of attention can be flexibly altered in STM to allow for adaptive behavior (Kuo, Stokes, & Nobre, 2012; Kuo, Rao, Lepsien, & Nobre, 2009; Theeuwes, Belopolsky, & Olivers, 2009; Awh, Vogel, & Oh, 2006; Lepsien & Nobre, 2006; Curtis & D'Esposito, 2003; Griffin & Nobre, 2003; Awh & Jonides, 2001). Spatial selection in mnemonic representations is known to influence perceptual encoding of external signals (Jha, 2002; Awh, Anllo-Vento, & Hillyard, 2000), which is consistent with the proposed functional and anatomical overlap of neural mechanisms mediating perceptual attention and STM (Gazzaley & Nobre, 2012; Theeuwes et al., 2009; Sörös et al., 2007; Awh et al., 2006; Müller & Knight, 2006; Naghavi & Nyberg, 2005; Pasternak & Greenlee, 2005; Curtis & D'Esposito, 2003; Awh & Jonides, 2001).

There are two lines of evidence suggesting an involvement of spatial attention in STM tasks: The attention-based rehearsal account states that covert spatial orienting to memorized locations supports the voluntary maintenance of spatial information (Theeuwes et al., 2009; Awh et al., 2006; Awh & Jonides, 2001; however, see also Belopolsky & Theeuwes, 2009a). The investigation of attention-based rehearsal therefore requires the implementation of spatial STM tasks, in which locations have to be memorized and,

thus, are directly task-relevant. A series of experiments using probe designs examined the influence of attention-based rehearsal on sensory encoding (Jha, 2002; Awh et al., 2000). In this context, probe refers to sensory events that probe the deployment of spatial attention and do not require a behavioral response. The studies mentioned above reported that, during retention, probes presented to memorized locations were preferentially encoded, compared with probes at nonmemorized locations. Such links between STM and perception suggest that spatial selection involves neural processes that are common to both domains.

Furthermore, spatial attention effects have also been reported in STM paradigms in which spatial attributes were not directly task-relevant, as memorization of locations for subsequent comparison with test stimuli was not required. These studies used retro-cues, presented after a set of spatially segregated sample stimuli (Astle, Scerif, Kuo, & Nobre, 2009; Kuo et al., 2009; Griffin & Nobre, 2003). As a consequence, physiological activity following retro-cues reflects control processes operating on mnemonic rather than external stimulus representations (see Lepsien & Nobre, 2006, for a review). Retro-cues that informed about the target sample via cueing of nonspatial (Astle et al., 2009; Kuo et al., 2009) or spatial attributes (Griffin & Nobre, 2003) caused lateralized electrophysiological activity indicative for the directionality of attention shifts in visual STM. This finding implies that STM preserves the spatial configuration of eliciting peripheral events (Astle et al., 2009; Kuo et al., 2009), even when memory for locations is not explicitly instructed. Moreover, this observation opens the intriguing possibility that retro-cues guiding

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selection in STM (retrospective selection) trigger shifts of spatial attention that might be unrelated to the voluntary maintenance of locations (attention-based rehearsal). In summary, retrospective selection and attention-based rehearsal are both associated with spatial attention but might represent functionally separable control processes, in other words, dissociable roles of spatial attention in STM. However, although all of the studies listed so far investigated the visual modality, retrospective selection has not been examined in touch up to today.

Evidence for a functional dissociation of retrospective selection and attention-based rehearsal has been observed in our previous somatosensory memory experiment (Katus, Andersen, & Müller, 2012). In a spatial STM task, participants received bilateral sample pulses followed by a retro-cue to control for exogenous orienting effects. The retro-cue consisted of a color change of the symmetrically shaped fixation cross, indicating whether the left- or right-hand sample was relevant for subsequent comparison with a single delayed test stimulus. Participants were asked to decide whether the test stimulus was applied to the same location (finger) as the retrospectively cued sample. The observed time course of spatial attention effects was rather unusual for attention-based rehearsal because the greatest spatial bias of encoding (indexed by the N140) was evident for early probes, presented shortly after the retro-cue. In vision, spatial STM experiments consistently reported sustained attention-based rehearsal effects (Awh et al., 2000, 2006; Jha, 2002). One might argue that such time-variant results are attributable to the tactile nature of the task in our study. Instead, we concluded that retrospective selection triggers transient attention shifts time-locked to the retro-cue, contributing to the sustained impact of attention-based rehearsal. It is important to point out that retrospective selection and attention-based rehearsal were confounded in the design of our previous experiment because participants were asked to memorize the retrospectively selected location. This confound is common to spatial STM paradigms, which therefore are problematic approaches to examine retrospective selection apart from possible attention shifts related to voluntary maintenance of locations (attention-based rehearsal) and spatial anticipation of test stimuli (more details in Katus et al., 2012).

The design of the task in this study differs from our earlier experiment in three key aspects. First and most importantly, participants were asked to memorize a non-spatial attribute, namely stimulus intensity, and locations of all tactile stimuli were unpredictable. This modification circumvents the drawbacks of spatial STM paradigms and rules out effects that might be attributable to attention-based rehearsal or spatial anticipation. If, nevertheless, retro-cues elicited transient attention shifts, this finding would substantiate the speculation that retrospective selection engages a time-variant control process linked to spatial attention yet dissociable from potentially confounding factors described above. Second, cue stimuli were uninformative as to the location of the target (i.e.,

sample) relevant for delayed comparison with the test stimulus. Tactile sample stimuli of different intensity were simultaneously applied to both hands, and the color change of the retro-cue indicated the category of the relevant sample stimulus in terms of intensity (weak vs. strong sample) rather than space (left vs. right hand). Third, we introduced a variable delay between samples and retro-cue to counter a systematic contamination of the N2pc to visual cues by neural responses to tactile sample stimuli. Our hypotheses focused on physiological measures sensitive to spatial selection between the left and right hands (somatosensory N140, e.g., Forster & Eimer, 2005) or hemifields (N2pc, e.g., Luck & Hillyard, 1994a).

Recent evidence suggests that the N2pc of the visual ERP (VEP) reflects selection in visual STM, that is, at a post-perceptual stage (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Kuo et al., 2009). In these studies, the N2pc was measured in response to centrally presented retro-cues that provided nonspatial information (e.g., shape and color) necessary to distinguish between targets and distracters within a set of spatially segregated sample stimuli. The N2pc indexed spatially specific access of information in visual STM, as this component reflected the location of the target sample (e.g., Kuo et al., 2009). Most intriguingly, selection in tactile STM modulated the N2pc to visual retro-cues in our earlier experiment. Such cross-modal links at a relatively early stage might shed light on the neural origins of the N2pc, suggesting contributions from neural processes that are, at least to some degree, detached from fundamental characteristics of the accessed information. Unfortunately, a decisive interpretation of the N2pc was compromised in our previous study because of a contamination by the P300 component to tactile sample stimuli.

The present somatosensory experiment sought to elucidate the neural mechanisms mediating retrospective selection between spatially segregated sample stimuli. Spatially specific biasing of neural activity in the period after retro-cues would point to an involvement of spatial attention in a scenario designed to avoid shortcomings of spatial STM paradigms, in particular, confounding factors such as attention-based rehearsal and spatial anticipation of test stimuli. We examined lateralized neural activity evoked by the visual retro-cue. Recent STM experiments reported modulations of the N2pc (Dell'Acqua et al., 2010; Kuo et al., 2009) and the anterior directing attention negativity (ADAN; see Griffin & Nobre, 2003). Consequently, such lateralized components were assumed to mirror selection in tactile STM. Second, attention shifts in STM influence selection in perception (Theeuwes et al., 2009; Awh et al., 2000, 2006; Jha, 2002; Awh & Jonides, 2001). The somatosensory N140 is reliably affected by spatial selection between the left and right hands in the perceptual domain (Forster & Eimer, 2004, 2005; Eimer, Forster, Fieger, & Harbich, 2004; Zopf, Giabbiconi, Gruber, & Müller, 2004; Eimer & Forster, 2003a; Michie, Bearpark, Crawford, & Glue, 1987; Josiassen, Shagass, Roemer, Ercegovic, & Straumanis, 1982; Desmedt & Robertson, 1977). Because

retrospective selection was associated with transient attention (Katus et al., 2012), we expected spatially specific encoding effects in a brief period after the retro-cue, influencing the N140 to probes but not to test stimuli. Furthermore, we examined the decision-related P300 component in response to tactile test stimuli. The P300 is greater for targets compared with distracters (Polich, 2007; Desmedt & Debecker, 1979), and because participants were asked to compare intensities, we expected enhanced P300 amplitudes when test stimuli were presented with the memorized relative to nonmemorized intensity. The spatial relation between cued sample and test stimulus did not convey useful information for the task (intensity comparison) and, thus, should not influence the P300. If retrospective selection is dissociable from attention-based rehearsal, electrophysiological measures (e.g., N2pc, ADAN, and N140) should mirror the location of the cued item, even when memorized attributes belong to a nonspatial feature dimension.

METHODS

Participants

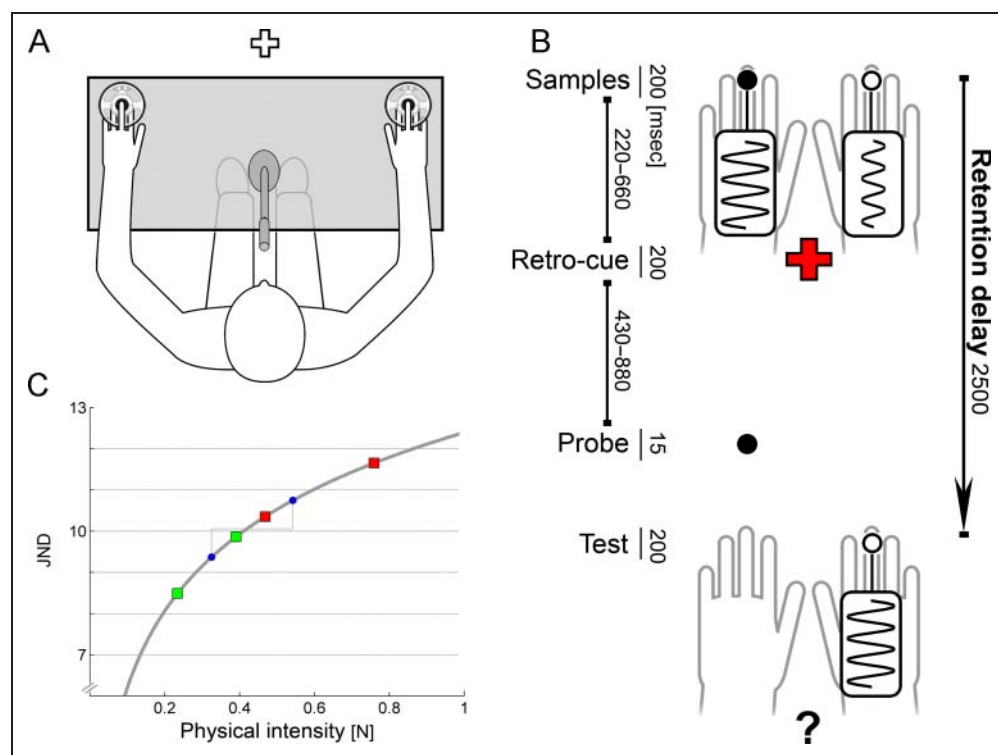
Twenty participants took part in the experiment. Two participants reported that they were unable to distinguish

between the samples' intensities in more than approximately one third of trials. Because of the resulting low performance, we excluded these participants from statistical analysis. A further participant ignored instructions and placed index rather than middle fingers on the stimulators during the last two blocks of the experiment. Seventeen participants remained in the sample (13 women, age range = 18–37 years, average = 25 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 Setup

The experimental setup is illustrated in Figure 1A. Tactile stimulation was provided by two miniature loudspeakers (Ekulit Elektrotechnik, Ostfildern, Germany) with cut-out membranes. Participants were asked to rest the distal phalanx of each middle finger on the inner plateau of a stimulator. This even part in the center of the speaker's basket forms the upper structural element of the magnetic core. Participants' index and ring fingers were located

Figure 1. Experimental paradigm. (A) Experimental setup: Tactile stimuli were delivered to the middle fingers' distal phalanges; both hands were covered from sight. Visual stimuli were shown on a monitor that could be seen through a window in the recording chamber. Retro-cues consisted of color changes of the white fixation cross to green or red. (B) Stimulation procedure: Tactile sample stimuli with different intensities were simultaneously applied to both hands. The color of the visual retro-cue informed about the intensity of the target sample, that is, weak versus strong. Participants were asked to compare intensity of cued sample and test, irrespective of their spatial relation. In the illustrated example, the red retro-cue determined the strong sample as target. Tactile events were either spatially congruent (black dots) or incongruent (white dots) relative to the location of the target sample. The exemplary trial required a "yes" response, because test and target had equal intensity. (C) Intensity scaling: Sample and test stimuli were scaled according to the Weber–Fechner Law. For each trial, a reference was randomly drawn from a predefined range of physical intensities (bounded by blue dots). The reference determined the intensity of both sample stimuli: Weak and strong samples were equidistantly below and above the reference, in terms of perceived intensity (y axis). In a given trial, sample stimuli differed by 1.7–2 JNDs. Throughout the experiment, intensities of weak and strong samples ranged between the green and red squares, respectively. Test stimuli were presented with the memorized intensity (50%) or differed by two JNDs (50%).



beneath the basket, providing a gentle upward pressure. Participants were encouraged to rest their middle fingers comfortably on the center plateaus. They were asked to neither lift the fingers upward nor press them against the stimulator. Participant's hands and stimulators were covered from sight by towels. Stimulators were located on additional towels on a table in front of the participant's chair. Distance between both hands was kept constant at 80 cm. White noise was presented via headphones to mask any sounds produced by the stimulators. Stimulators were driven by a dual channel amplifier connected to a digital-to-analog conversion card. Stimulation was controlled by MATLAB (The MathWorks, Natick, MA).

Task Design and Stimulation Material

Stimulation Procedure and Task

Participants received bilateral sample stimuli with differing intensities. Participants were instructed to selectively memorize the intensity of a single retrospectively cued sample (target) for subsequent comparison with a test stimulus. The target sample was determined by the categorical cueing of a nonspatial stimulus attribute, namely intensity. Spatial properties of all tactile stimuli were unpredictable and without influence on the required response. Figure 1B illustrates the stimulation sequence. A trial started with simultaneous presentation of bilateral tactile sample stimuli. Between 220 and 660 msec after sample offset, the fixation cross changed its color for 200 msec, thereby serving as retro-cue. The retro-cue informed about the intensity category (weak, strong) of the to-be-memorized sample via an arbitrary color-mapping rule. A probe stimulus was randomized to either hand between 430 and 880 msec after retro-cue offset. Participants had been informed in advance that probes were task-irrelevant. A unilateral test stimulus was presented to the left (50%) or right (50%) hand at a fixed latency of 2500 msec after sample onset. Test stimuli were either presented with the same physical intensity as the cued sample (50%) or scaled to a nonmemorized intensity (50%). A question mark prompted participants to respond verbally during the subsequent 1500-msec period. Participants were instructed to compare the intensity of the test stimulus with the retrospectively cued sample, regardless of their spatial relation. Participants were asked to say the vowel "a" (corresponding to a "yes" response) if intensities matched and "i" if they differed ("no" response). The response period ended when the question mark was replaced by the fixation cross. Between 400 and 500 msec thereafter, the next trial started.

The main experiment consisted of 560 trials divided into eight blocks, approximately 6 min and 30 sec each. Feedback on average hit and false alarm rates was provided after each block. Before recordings, three to five training blocks of 50 trials were performed until stable performance was reached. During the main experiment, participants

were instructed to avoid head and arm movements and maintain fixation while the cross was present.

Tactile and Visual Stimuli

Mechanical tactile stimulation involved samples, probes, and test stimuli. Sample and test stimuli consisted of 200-msec-long vibrotactile sinusoids, driven at 200 Hz. The intensity of sample and test stimuli varied across experimental trials; the intensity scaling procedure will be described below (Psychometric Scaling of Intensities section). A sample pair consisted of a weak and strong stimulus, simultaneously applied to the left and right hands. The spatial configuration of sample pairs was unpredictable: Sample stimuli with a specific intensity (e.g., strong) were equiprobably presented to the left or right hand. Unilateral test stimuli were randomized to the left (50%) or right (50%) hand. Tactile probe stimuli consisted of concise 15-msec pulses at 200 Hz, that is, two successive 5-msec pulses separated by a 5-msec delay. Probes were presented with fixed intensity of 0.84 N and randomized to the left (50%) or right (50%) hand. Probes were not delivered in 17% of the trials to reduce predictability of the stimulation procedure.

Color change of the white fixation cross to either green or red served as retro-cue. The symmetric retro-cue was centrally presented on the monitor for 200 msec. At a given viewing distance of 140 cm, the retro-cue had a size of 1.23° of visual angle. One of two mapping rules was randomly assigned to each participant before the experiment. Ten participants received the instruction to memorize the weak versus strong sample stimulus when the retro-cue turned green versus red, respectively. For the remaining seven participants, this mapping rule was reversed (i.e., red and green cued weak and strong samples, respectively). The number of trials with green or red cues was balanced for a particular spatial configuration of sample intensities. Within a given subject, the same color cued tactile samples at the left (50%) and right (50%) hands.

Psychometric Scaling of Intensities

The scaling of tactile sample and test stimuli was based on a psychometric function (see Figure 1C), which had been approximated according to the Weber-Fechner Law with help of four nonnaive participants (staff members) before the experiment. Parameters of the transfer function, such as the Weber fraction and absolute threshold, were obtained using QUEST (Watson & Pelli, 1983), a Bayesian adaptive psychometric method. The scaling of sample stimuli had to ensure that participants (a) were able to discriminate between bilaterally presented samples in terms of intensity and (b) memorized sensory signals rather than abstract category labels. For a given trial, the scaling of tactile stimuli was based on a reference intensity randomly drawn from a range of physical intensities, specifically 0.32–0.54 N (blue circles in Figure 1C). The

reference determined the intensities of both sample stimuli. Sample pairs differed between 1.7 and 2 just noticeable differences (JNDs) and were equidistant with respect to the reference intensity, for example, one JND below and above the reference in terms of perceived intensity. Green and red squares in Figure 1C represent the total range of weak and strong sample intensities across experimental trials, respectively. With equal probability, test stimuli were scaled to the intensity of the target or differed by approximately two JNDs. For the majority (75%) of nontarget test stimuli, intensities were biased toward the uncued intensity category: Weak nontargets exceeded the memorized intensity, whereas strong nontargets were set to a weaker intensity. This constraint sought to discourage participants to memorize the intensity of the distracter along with the target.

Data Recording and Analysis

Recording of Electrophysiological Data and Treatment of Artifacts

Participants were seated in a comfortable chair in a dimly lit electrically shielded chamber. 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). During recordings, all scalp channels were referenced to an electrode next to POz. A bipolar outer canthus montage (HEOG) monitored lateral eye movements. A bipolar montage below and above the right eye (VEOG) recorded vertical eye movements and blinks. Data processing was performed off-line with the help of the EEGlab toolbox (Delorme & Makeig, 2004) and custom-written MATLAB routines. Continuous EEG data were digitally band-pass filtered (0.5–40 Hz, Kaiser windowed finite impulse response). Somatosensory evoked potentials (SEPs) in response to tactile probe and test stimuli were segmented into 500-msec epochs, starting 100 msec before stimulus onset and ending 400 msec after stimulus onset. VEPs elicited by visual retro-cues were epoched into 800-msec periods, starting 100 msec before cue onset and extending 700-msec postcue. A 100-msec prestimulus baseline was subtracted from SEPs and VEPs.

Trials with horizontal eye movements exceeding 25 μ V (roughly corresponding to 2° of visual angle) were rejected before further artifact correction procedures. The influence of eye blinks on the EEG signal was corrected by means of independent component analysis (Bell & Sejnowski, 1995). Independent components associated with eye blinks are known to have stereotypical scalp topographies and frequency characteristics (Delorme, Sejnowski, & Makeig, 2007). Such components were identified by visual inspection and subtracted from the data set. Subsequently, epochs exceeding a voltage threshold of $\pm 150 \mu$ V were rejected. The remaining data were subjected to SCADS (statistical control of artifacts in dense array EEG/magnetoencephalography studies; see Junghöfer, Elbert, Tucker, & Rockstroh, 2000). SCADS identified artifacts on the basis of statistical parameter distributions obtained from a given data set. Spherical spline interpolation of artifact-free electrodes was used to correct contaminated signals. Epochs with more than 12 artifactual electrodes were rejected. On average, 6%, 6.2%, and 4.2% of all epochs to cue, probe, and test stimuli were rejected, respectively. These rejection rates did not differ between experimental conditions. After artifact correction and rejection, the EEG signal was rereferenced to the arithmetic mean of both mastoids. To ensure that data were not influenced by small but systematic eye movements, which might have escaped the above 25- μ V threshold, HEOG waveforms were separately averaged for trials in which the retro-cue indicated the left- versus right-hand sample. A paired *t* test running across sampling points postcue revealed no difference between these trials during the analyzed time windows.

Analysis of Electrophysiological Data

Table 1 summarizes latency range and electrode selection used for the acquisition of specific VEP and SEP components. The stated parameters were chosen in accordance with previous findings with regards to N2pc (Dell'Acqua et al., 2010; Kuo et al., 2009) and N140 (e.g., Forster & Eimer, 2005). Additional analyses assessed modulations of the ADAN (see Forster, Sambo, & Pavone, 2009; Griffin & Nobre, 2003; van Velzen, Forster, & Eimer, 2002); the

Table 1. Time Window and Electrode Selection for the Measurement of VEP and SEP Components

<i>Eliciting Stimulus</i>	<i>Component</i>	<i>Electrodes</i>	<i>Latency Range (msec)</i>
Retro-cue (VEP)	N2pc	P7/8, P5/6, PO7/8	250–310
Retro-cue (VEP)	ADAN	F3/4, F5/6, FC5/6	350–700
Probe, test (SEP)	N140	FC5/6, C5/6, CP5/6	124–156
Probe, test (SEP)	Nd200	FC5/6, C5/6, CP5/6	184–216
Test (SEP)	P300	CPz, Pz, POz	260–340

Mean amplitudes in the stated latency ranges entered statistical testing. All components were measured at contralateral and ipsilateral ROIs, except for the P300.

Nd200, a negative difference wave emerging at around 200-msec poststimulus (cf. Gillmeister & Forster, 2012; Forster & Eimer, 2004; Eimer & Forster, 2003b); and the P300 (Polich, 2007; Desmedt & Debecker, 1979).

Statistical analyses were conducted on the average of three neighbored electrodes, as illustrated in Figure 2. The design factor electrode cluster was included in the analyses of VEP and SEP components, except for the P300 that was measured at a single ROI. VEPs and SEPs acquired at a particular electrode cluster were averaged across both hands, because preliminary analyses of electrophysiological and behavioral data revealed no significant differences dependent on the location of the cued sample stimulus. Mean amplitudes were calculated for the time windows specified in Table 1 and submitted to repeated measures ANOVAs. Statistical analyses included trials with correct and incorrect behavioral responses because these did not differ with regards to the modulation of physiological measures under investigation. Within-subject confidence intervals (CIs) in figures reflect the error terms associated with particular effects of interest, independent of between-subject variance (see Jarmasz & Hollands, 2009; Loftus & Masson, 1994). Here, conditional means with nonoverlapping CIs represent a significant effect ($p < .05$) of the experimental manipulation specified in the respective figure caption.

Lateralized components of the VEP. Separate two-way ANOVAs assessed lateralized VEP components to retro-cues, such as N2pc and ADAN. The statistical design comprised the factors of Electrode Cluster (relative to cued sample: contralateral, ipsilateral) and Cued Intensity (weak, strong). Importantly, Electrode Cluster main effects reflect differential activity related to the location of the target sample.

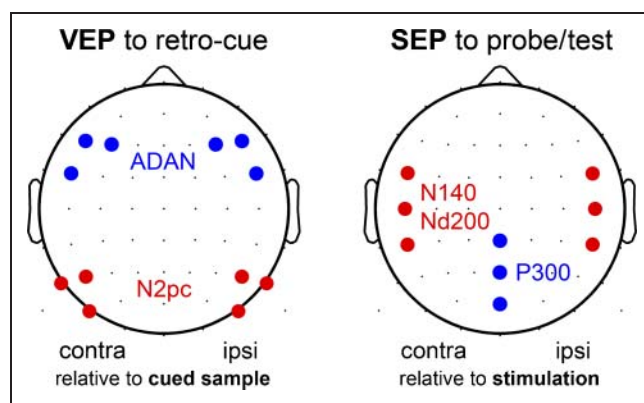


Figure 2. Electrode selection. Electrode clusters defined for statistical assessment of VEPs (left) and SEPs (right). Three neighboring electrodes were averaged for a particular recording cluster. Each VEP/SEP component was measured at symmetrical contralateral and ipsilateral electrode clusters, except for the P300 of the SEP. Contra = contralateral; ipsi = ipsilateral.

SEP components elicited by probe stimuli. Modulations of the SEP to task-irrelevant probe stimuli occurred during the latency range of the N140 and Nd200. Separate three-way ANOVAs tested the influence of the design factors Spatial Congruency (spatial relation with respect to the cued sample: congruent, incongruent), Stimulation Sequence (intensity of sample stimulus preceding the probe: weak, strong), and Electrode Cluster. Stimulation sequence served as a control factor for prior exposure to weak versus strong stimulation at a given finger. Most importantly, we hypothesized that selection in tactile STM leads to spatially specific sensory encoding, reflected by spatial congruency main effects.

SEP components elicited by test stimuli. Separate three-way ANOVAs assessed the SEP in response to task-relevant test stimuli at latencies corresponding to the N140 and Nd200. The statistical design comprised the factors of Spatial Congruency (congruent, incongruent), Intensity Congruency (target, distracter), and Electrode Cluster. Intensity congruency compared test stimuli with memorized versus nonmemorized intensity. The P300 component was obtained from a single recording cluster and assessed by a two-way ANOVA with factors of Intensity Congruency and Spatial Congruency.

Recording and Analysis of Behavioral Data

Vocal responses during the 1500-msec response period were recorded by a microphone located in front of the participant. Voice key routines written in MATLAB code analyzed speech signals with respect to their formant characteristics. Estimated resonance frequency profiles of the first two formants were categorized by means of multinomial logistic regression. Regression parameters had been individually determined for each participant in a calibration session at the beginning of the experiment. Categorizations were checked again off-line and corrected if necessary. “Yes” and “no” responses were associated with the vowels “a” and “i,” respectively. A hit was defined as “yes” response, given that the test stimulus was presented with the target intensity. A correct rejection was considered as “no” response following a distracter, that is, test with nonmemorized intensity. Hit and correct rejection rates were submitted to separate repeated-measures ANOVAs comprising the factors of Cued Intensity (weak, strong), Probe Congruency (congruent, incongruent, no probe), and Test Congruency (congruent, incongruent). Note that congruency referred to the spatial relation between a particular stimulus and a target sample. The location of the cued sample (left vs. right hand) was not included as a factor because preliminary analyses did not find significant differences in hit as well as correct rejection rates.

RESULTS

Behavioral Data

Hit rates were higher when both the cued sample and test stimulus had been presented to the same hand compared with different hands (test congruency: $F(1, 16) = 6.01$, $p = .026$). This effect was driven by responses to targets of strong intensity and was absent for weak targets (Cued Intensity \times Test Congruency: $F(1, 16) = 8.57$, $p = .010$). No further effects or interactions were observed in hit rates. The analysis of correct rejection rates revealed a different pattern. No significant effects or interactions were found except for performance differences that depended on the cued intensity category. Participants more often responded correctly when the target intensity was weak as compared with strong (cued intensity: $F(1, 16) = 16.55$, $p = .001$).

Electrophysiological Data

Lateralized Activity after Retro-cues (VEP)

Figure 3A shows the VEP to visual retro-cues, recorded at posterior scalp regions contralateral and ipsilateral to the target sample. A highly significant N2pc modulation mirrored the location of the retrospectively cued sample, indicated by more negative amplitudes in the N2pc time range contralateral to the target as compared with ipsilateral (electrode cluster: $F(1, 16) = 24.78$, $p < .001$). This effect generalized across retro-cues that directed attention to weak versus strong samples, as an interaction between electrode cluster and cued intensity was not significant ($p > .1$). The topographical extent of the N2pc modulation is shown in the difference map, Figure 3B. Posterior lateralized activity was accompanied by the ADAN, a differential negativity contralateral to the cued sample (electrode cluster: $F(1, 16) = 5.92$, $p = .027$). There was no significant interaction of electrode cluster and cued intensity in the ADAN time range ($p > .1$). Taken together, retro-cues elicited lateralized activity over posterior and anterior scalp regions, which consistently reflected selection in tactile STM.

Components of the SEP to Probe Stimuli

Figure 4A shows SEPs to task-irrelevant probe stimuli, recorded contralateral and ipsilateral to stimulation. The N140 latency range is marked in these graphs because major predictions were based on this component. Figure 4B depicts scalp distributions of N140 and Nd200 along with the topographic extent of spatial congruency effects in these time ranges.

Somatosensory N140. The N140 was subject to the spatial relation between probe stimulus and target sample. Probes presented to the same hand as the retrospectively

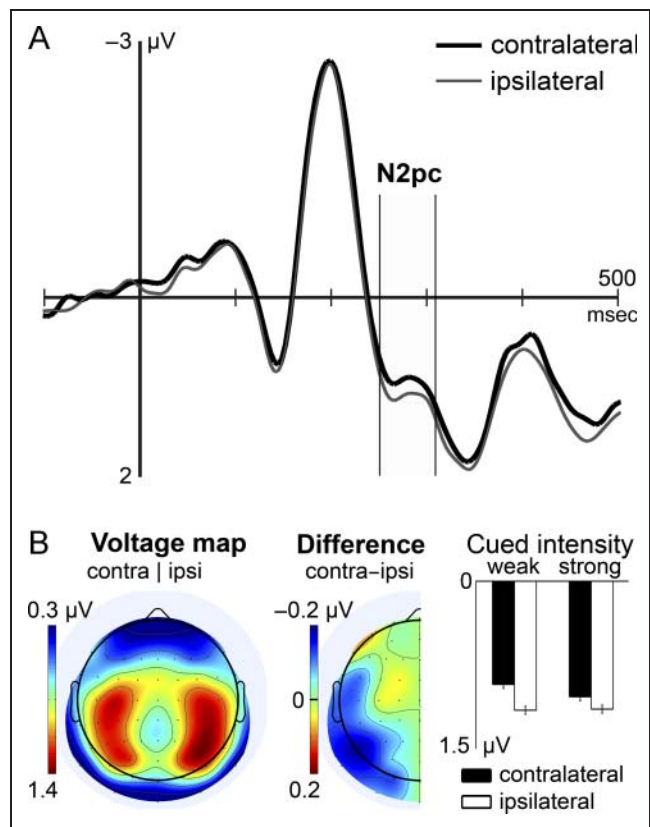


Figure 3. (A) Grand mean VEP to retro-cues measured at posterior scalp regions contralateral (thick black line) and ipsilateral (thin gray line) to the retrospectively cued sample. Negative values above midline. (B) Grand mean isocontour voltage map (left column), difference map (middle), and mean amplitudes (right) during the N2pc latency range. The arrangement of data in the voltage map is equivalent to the cueing of the right-hand sample. Contralateral and ipsilateral electrodes correspond to left and right scalp regions, respectively. The difference map illustrates amplitudes of contralateral minus mirrored ipsilateral recordings; redundant parts are omitted. The right column shows mean amplitudes in the N2pc latency range measured contralateral (black bars) and ipsilateral (white bars) to the target sample, grouped by the cued intensity category. Error bars depict within-subject CIs associated with the main effect of electrode cluster. Note the differing scales of voltage maps and bar plots. Contra = contralateral; ipsi = ipsilateral.

cued sample elicited an enhanced N140 as compared with probes delivered to the other hand (Spatial Congruency: $F(1, 16) = 8.30$, $p = .011$). The influence of spatial congruency on the N140 was comparable across recording sites, although in tendency greater contralateral to stimulation (Spatial Congruency \times Electrode Cluster: $F(1, 16) = 3.19$, $p = .093$). Probes elicited greater contralateral and smaller ipsilateral N140 amplitudes when the preceding weak sample was presented to the same hand and the strong sample to the opposite hand (Stimulation Sequence \times Electrode Cluster: $F(1, 16) = 7.08$, $p = .017$). No further effects or interactions were significant, except for the well-known asymmetry of N140 amplitudes toward scalp regions contralateral to

stimulation (Electrode Cluster: $F(1, 16) = 6.27, p = .024$). Thus, selection in STM influenced the N140. Probes with congruent spatial attributes as the selected item elicited an enhanced N140, as compared with incongruent probes. This modulation was independent of effects related to the stimulation sequence used in the present experiment.

Negative difference wave (Nd200). Spatial congruency led to a near-significant modulation of the Nd200. Probe stimuli with congruent spatial properties tended to result in more negative amplitudes compared with incongruent probes (spatial congruency: $F(1, 16) = 4.31, p = .055$). This modulation was predominantly found contralateral to stimulation, as indicated by a significant interaction between spatial congruency and recording site (Spatial

Congruency \times Electrode Cluster: $F(1, 16) = 5.46, p = .039$). No further effects were found in the Nd200 latency range, except for a tendency of amplitude differences across contralateral and ipsilateral regions (Electrode Cluster: $F(1, 16) = 4.43, p = .052$).

Components of the SEP to Test Stimuli

Figure 5A shows SEP waveforms in response to tactile test stimuli, recorded at scalp regions over somatosensory areas contralateral and ipsilateral to stimulation. N140 amplitudes did not differ for test stimuli presented to the same or different hand as the cued sample (Spatial Congruency: $F(1, 16) = 0.51, p > .1$); compare with Figure 4B. Furthermore, the N140 was not significantly different for test stimuli with memorized as compared with nonmemorized intensity (Intensity Congruency: $F(1,$

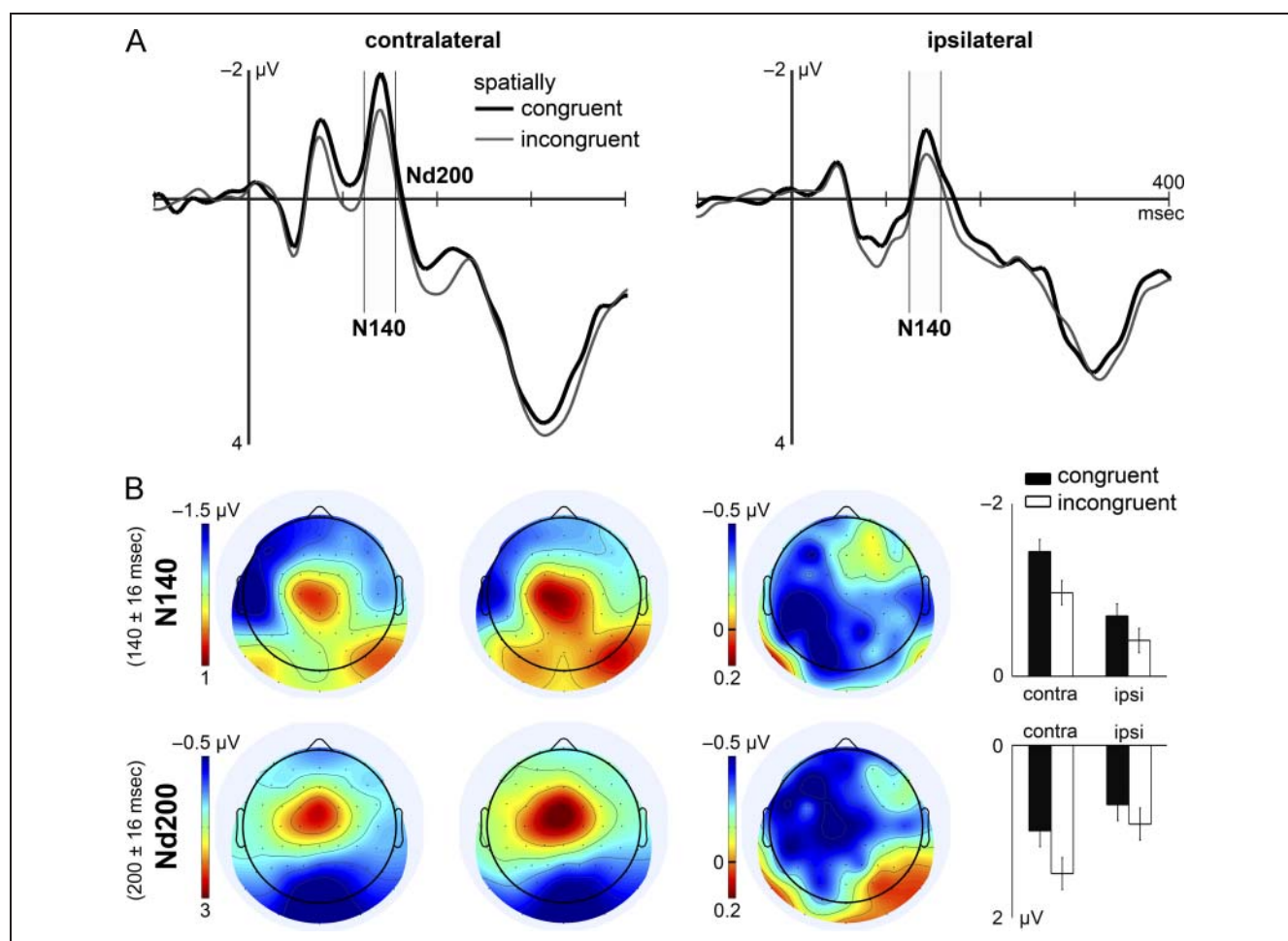


Figure 4. (A) Grand mean SEPs to task-irrelevant tactile probe stimuli recorded at parietal electrodes contralateral (left) and ipsilateral (right) to stimulation. Spatially congruent probe stimuli were presented to the same hand as the cued sample (bold black line), whereas incongruent probes were delivered to the other hand (thin gray line). (B) Separate rows represent averages during the latency ranges of N140 and Nd200. Columns from left to right illustrate grand mean isocontour voltage maps for congruent and incongruent probes, difference map, and mean amplitudes in the particular latency range. The arrangement of data in voltage maps corresponds to stimulation of the right hand. The difference map represents congruent minus incongruent probe stimulus topographies. The right graph shows mean amplitudes in response to spatially congruent (black bars) and incongruent (white bars) probe stimuli. Within-subject CIs are based on spatial congruency main effects, which were separately estimated for N140 and Nd200. Note the differing scales of voltage maps and bar plots. Contra = contralateral; ipsi = ipsilateral.

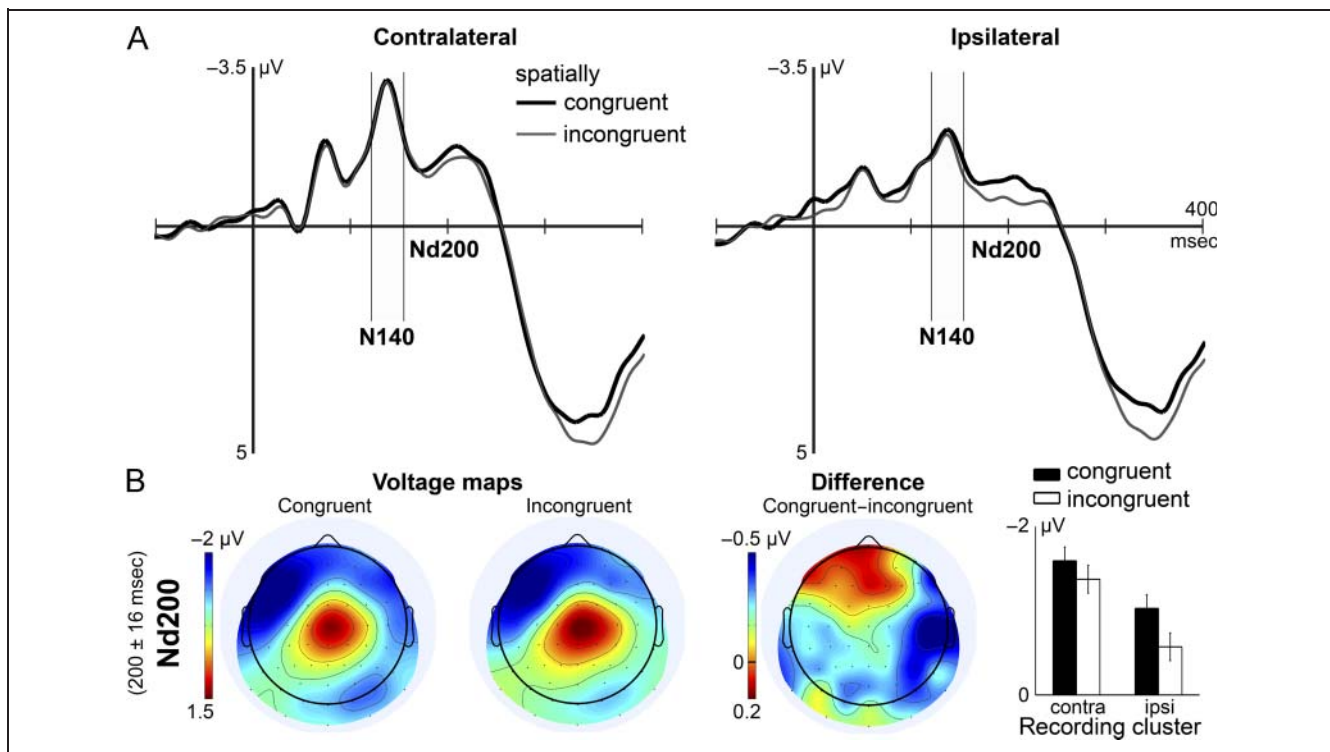


Figure 5. (A) Grand mean SEPs to task-relevant tactile test stimuli acquired at parietal electrodes contralateral (left) and ipsilateral (right) to stimulation. Spatially congruent test stimuli were presented to the same hand as the cued sample (bold black line), whereas incongruent tests were delivered to the other hand (thin gray line). (B) From left to right: grand mean voltage maps, difference map, and averaged amplitudes in the latency range of the Nd200. The arrangement of data corresponds to stimulation of the right hand. The difference map represents subtracted topographies to congruent minus incongruent test stimuli. The right graph depicts mean Nd200 amplitudes elicited by spatially congruent (black bars) and incongruent (white bars) test stimuli, measured contralateral and ipsilateral to stimulation. Within-subject CIs are based on the spatial congruency main effect for test stimuli. Note the differing scales of voltage maps and bar plots.

16) = 0.00, $p > .1$). Except for amplitude differences across recording sites (Electrode Cluster: $F(1, 16) = 15.52$, $p = .001$), no further effects were present during the N140 latency range. The spatial relation between cued sample and test stimulus resulted in a significant modulation of the Nd200: Amplitudes were more negative when test and cued sample were presented to the same hand compared with different hands (spatial congruency: $F(1, 16) = 4.75$, $p = .045$). No further effects or interactions were present for the Nd200, except for amplitude differences between contralateral and ipsilateral recordings (electrode cluster: $F(1, 16) = 10.59$, $p = .005$).

Participants were instructed to compare intensity of cued sample and test stimulus. The P300 to tests was the only component sensitive to congruency in terms of the task-relevant feature dimension, intensity. The P300 was enhanced when test stimuli were scaled to memorized intensity compared with distracter intensity (Intensity Congruency: $F(1, 16) = 7.55$, $p = .014$). In contrast, the P300 was insensitive to the spatial relation between cued sample and test stimulus (Spatial Congruency: $F(1, 16) = 0.01$, $p > .1$). Intensity congruency affected the P300 to a greater degree when test and cued sample were presented to the same hand, as indicated by a significant interaction between both factors

(Intensity Congruency \times Spatial Congruency: $F(1, 16) = 7.92$, $p = .012$).

DISCUSSION

This study examined effects of spatial attention in tactile retrospective selection. The paradigm was designed to rule out attention-based rehearsal: Because the delayed judgment involved a comparison of intensities rather than locations, the attention-based rehearsal account would not predict spatially specific biasing of neural activity. However, visual retro-cues elicited lateralized components (N2pc, ADAN) that mirrored the location of the target sample. Somatosensory processing during the retention period was also subject to a spatial encoding bias (indexed by the N140), favoring probes that were delivered to the same location as the cued sample. Contrary to that, spatial congruency did not affect the N140 to test stimuli, indicating that spatial attention was not directed to one or the other side at the end of the trial. These findings substantiate the interpretation that retrospective selection leads to transient attention shifts, as opposed to the sustained impact of attention-based rehearsal (Awh et al., 2000, 2006; Jha, 2002). Because the memorization of locations was not explicitly required, we conclude that

retrospective selection is mediated by a time-variant process that is functionally dissociable from attention-based rehearsal.

Neural Mechanisms of Retrospective Selection

Convergent modulation of physiological measures evoked by visual and tactile stimuli suggests that retro-cues trigger focal attention shifts toward the location of the target sample. Notably, we focused on electrophysiological measures sensitive to locations rather than nonspatial features or objects. For the interpretation of spatial attention effects, it is important to remind that this study adopted a design in which target and distracter sample were associated with distinct locations (Dell'Acqua et al., 2010; Kuo et al., 2009; Griffin & Nobre, 2003). Our results demonstrate that the neural circuitry mediating the retrospective selection of nonspatial information is linked to spatial attention mechanisms.

One interpretation of the transient time course of spatial attention effects in retrospective selection observed here and in our previous study (Katus et al., 2012) is that a decay of spatial attributes in STM leads to attenuation of spatially specific measures. However, our results show that spatial attributes in STM are preserved throughout the entire retention delay, as the Nd200 component to tactile probe as well as test stimuli reflected the location of the cued sample. Thus, we conclude that transient spatial attention effects reflect the engagement of a time-variant executive process.

The ADAN mirrors selection in tactile STM, and this finding is in line with evidence from vision (Griffin & Nobre, 2003). Moreover, the ADAN modulation points to the involvement of supramodal networks of selective attention (Eimer et al., 2004; Eimer & van Velzen, 2002; van Velzen et al., 2002). Mechanisms of supramodal attention assert top-down biasing signals that regulate activity in modality-specific regions (Sambo & Forster, 2011; Lakatos et al., 2009). Because probe stimuli were presented after the retro-cue, it seems plausible that supramodal influences contributed to the modulation of the somatosensory N140. Yet, high-level biasing signals generated in the ADAN time range cannot explain cross-modal effects at a preceding latency: The N2pc to visual retro-cues mirrors spatially specific access of information in tactile STM. Similar results have been reported in purely visual STM experiments (Dell'Acqua et al., 2010; Kuo et al., 2009). Hence, the N2pc appears to index a selective process that is, at least partially, detached from the nature of mnemonic content.

Cue-related Activity

Visual retro-cues elicited the lateralized N2pc and ADAN components, which consistently indicated the location of the cued sample. Unlike our previous experiment, retro-cues did not inform about the location of the relevant

sample here, and for each participant, the same physical stimulus cued samples at the left and right hands with equal probability. Our findings support the notion that retrospective selection engages spatially specific biasing mechanisms with similarity to those involved in the processing of peripheral events, for example, in visual search (N2pc, cf. Kuo et al., 2009) or anticipatory attention tasks (ADAN; cf. Griffin & Nobre, 2003). Most interestingly, symmetric retro-cues elicited the N2pc, an observation extending mere replication of a phenomenon described previously (Dell'Acqua et al., 2010; Kuo et al., 2009), because retrospective selection was based on mnemonic representations of tactile rather than visual signals. Our results show that the N2pc is sensitive to selection in STM, even when the accessed information is related to a non-visual modality.

The N2pc is thought to originate in occipito-temporal regions, presumably in extrastriate visual cortex (Oostenveld, Praamstra, Stegeman, & van Oosterom, 2001; Luck & Hillyard, 1994a, 1994b). Sources downstream to visual sensory areas are known to contribute to the N2pc: Hopf et al. (2000) reported engagement of parietal regions preceding activity in occipito-temporal cortex. The authors related the early parietal source to neural networks controlling the directionality of attention shifts. Cohen, Heitz, Schall, and Woodman (2009) demonstrated that feedback from FEF neurons influences the generation of the macaque N2pc homologue in posterior cortical regions. In aggregate, these findings point toward a hierarchy of neural processes shaping the N2pc. Top-down influence from attentional control structures might regulate sensory-specific mechanisms in visual cortex, such as spatial filtering of visual signals (e.g., Hopf et al., 2000). In accordance with findings in vision (Dell'Acqua et al., 2010; Kuo et al., 2009), we show that N2pc effects can be obtained in absence of lateralized visual events, supporting the view that the N2pc is sensitive to selection at a postperceptual stage. The early engagement of posterior regions points to an involvement of neural processes related to the visual system.

Spatial attributes of tactile events are describable in terms of anatomical and extrapersonal coordinates because touch operates on separable—yet linked—spatial reference frames (Sambo & Forster, 2011; Heed & Röder, 2010; Eimer, Forster, & van Velzen, 2003). The N2pc is primarily associated with vision where spatial selection is based on an extrapersonal frame (Sambo & Forster, 2011). Visual space is furthermore of relevance for neural structures guiding eye movements, such as the FEFs (Bisley, 2011; van der Lubbe, Neggers, Verleger, & Kenemans, 2006; Corbetta, 1998) and the superior colliculus (e.g., Belopolsky & Theeuwes, 2011). Saccade studies provided evidence for an active role of the oculomotor system in STM tasks that involve retrospective selection (Belopolsky & Theeuwes, 2011) as well as attention-based rehearsal (Belopolsky & Theeuwes, 2009b). The overlap between eye movements, spatial attention, and spatial STM in vision is consistent with

the notion that these domains rely on common spatial codes (Theeuwes et al., 2009). This study demonstrates that the N2pc to visual retro-cues mirrors selection in mnemonic representations of tactile signals. We speculate that such early cross-modal links are attributable to the common coding of extrapersonal coordinates in touch and vision.

Processing of Somatosensory Events

The analyses of tactile stimuli (probes, tests) revealed two results of interest. First, a spatial bias in tactile encoding (indexed by the N140) was evident for probes but not for test stimuli. This finding is consistent with the proposal that, unlike attention-based rehearsal, retrospective selection leads to transient fluctuations of spatial attention time-locked to the retro-cue (Katus et al., 2012). Second, spatial congruency influenced the SEP to test stimuli at latencies before intensity congruency, indicating that spatial and nonspatial attributes were evaluated in a sequential fashion. Because we examined the role of spatial attention in retrospective selection, we first discuss spatial congruency effects (e.g., N140) before we address modulations of intensity congruency (P300).

The somatosensory N140 is a reliable marker of spatial selection between the left and right hands in perception (Forster & Eimer, 2004, 2005; Eimer et al., 2004; Zopf et al., 2004; Eimer & Forster, 2003a; Michie et al., 1987; Jossiasen et al., 1982; Desmedt & Robertson, 1977). In the present experiment, the N140 to probe stimuli mirrored the location of the cued sample: Amplitudes were enhanced when sample and probe were presented to the same hand, relative to different hands. Spatial congruency did not affect the N140 to test stimuli. In summary, these findings suggest that retrospective selection guides sensory encoding for a brief period after the retro-cue. In our previous spatial STM study, greatest attentional N140 modulations were observed for probes that were presented early after the retro-cue, as compared with late in the retention delay. Here, the timing of probe stimuli roughly corresponds to the latencies of such early probes. We replicate a transient spatial encoding bias because of selection in STM in a paradigm that did not explicitly require spatial STM, specifically the maintenance of a location for subsequent comparison with a delayed stimulus.

Test stimuli of memorized intensity led to higher hit rates when test and cued sample were presented to the same hand, compared with different hands. Does this behavioral finding suggest that retrospective selection leads to sustained—rather than transient—spatial attention effects? Notably, hit rates are associated with responses to targets (memorized intensity), whereas correct rejections relate to distracters (nonmemorized intensity). However, the enhancement of hit rates was not accompanied by a comparable modulation of the proportion of correct rejections. It is implausible to assume that spatial attention was deployed in a sustained fashion in half of the ex-

periment (targets) and transiently in the remaining trials (distracters), because test stimuli of memorized and nonmemorized intensities were presented in a random sequence. Moreover, the N140 component is a reliable marker of spatially specific encoding (e.g., Forster & Eimer, 2005). If test stimuli with target but not distracter intensity were subject to a spatial encoding bias, the N140 should reflect an interaction between spatial congruency and intensity congruency, which was not the case. Instead, we found no physiological evidence for spatially specific encoding at the end of the retention delay.

The spatial congruency effect in hit rates might be attributable to sensitivity differences between the dominant and nondominant hands: The recognition of a memorized intensity (target) should be easier when the sensory system (hand) is kept constant. Otherwise, the altered sensory system might introduce variability in the sensation elicited by a particular physical intensity. In light of these considerations, we presume that the spatial congruency effect on hit rates is not caused by perceptual spatial attention. The N140 to probe stimuli exhibited a spatial encoding bias, but the N140 to test stimuli did not. The absence of a spatial encoding bias for test stimuli suggests that, at the end of retention, spatial attention was equally divided between the left and right hands. This is not surprising because spatial randomization of test stimuli eliminates a confounder in spatial STM paradigms: the conceivable strategy to anticipate test stimuli at memorized locations.

As to test stimuli, the experimental design manipulated congruency in separate feature dimensions, space and intensity. The task required a delayed comparison of intensities rather than locations. Hence, only nonspatial attributes of test stimuli conveyed crucial information for the judgment. It is established that the decision-related P300 is enhanced for target stimuli as compared with distracters (Sambo & Forster, 2011; Polich, 2007; Desmedt & Debecker, 1979). Intensity congruency modulated the P300, leading to enhanced amplitudes when tests were scaled to memorized relative to nonmemorized intensity. In contrast, spatial congruency did not affect the P300. Accordingly, the P300 reflects attributes of task-relevant features but not attributes of feature dimensions that are arbitrary for a cognitive decision.

Are the Nd200 and P300 indicative for successive phases in the evaluation of tactile information? Interestingly, numerous somatosensory studies that found a relative negativity around 200-msec poststimulus did not report an enhanced P300 for targets as compared with distracters (Gillmeister & Forster, 2012; Forster & Gillmeister, 2011; Gillmeister, Adler, & Forster, 2010; Forster & Eimer, 2004; Eimer & Forster, 2003b). This observation led to the speculation that the negative difference wave represents a reversed attention effect at longer latencies (Sambo & Forster, 2011). Here, the P300 was clearly separable from the rather short-lived Nd200 modulation, and more importantly, these long latency components mirrored congruency in separate feature dimensions of space

(Nd200) and intensity (P300). The Nd200 was only sensitive to the task-irrelevant feature dimension, with a consistent pattern of modulation across behaviorally irrelevant probes and test stimuli that required decision and response. One speculation is that the Nd200 reflects a phase of rapid evaluation of stimulus properties against templates in STM before an exhaustive processing of task-relevant information and decision (indexed by the P300). This interpretation would be consistent with the finding that the Nd200 attenuates when participants attend to two locations, relative to a single location (Eimer & Forster, 2003b). In summary, spatial congruency and intensity congruency modulated successive components of the SEP to test stimuli. This result points to an asynchronous processing of spatial and nonspatial attributes (but, see Forster & Eimer, 2004).

General Conclusions

The focus of attention can be flexibly altered in STM (Lepsien & Nobre, 2006). Retro-cues that inform about a nonspatial attribute of the target sample initiate a cascade of spatially specific biasing signals indicative for the target's location. Retrospective selection affects markers of spatial attention with neural origins in posterior (N2pc), anterior (ADAN), and fronto-parietal (N140) networks. Intensity information is accessed in a spatially specific fashion, which demonstrates that spatial properties are preserved in mnemonic representations, even if memory for locations is not explicitly instructed (Astle et al., 2009; Kuo et al., 2009).

The earliest influence of retrospective selection was found at posterior scalp regions: The N2pc to visual retro-cues is sensitive to selection in tactile STM, and this effect is not attributable to the physical asymmetries of cue stimuli (cf. van Velzen & Eimer, 2003). We speculate that the N2pc reflects involvement of early selection mechanisms that operate on coordinates in external space. Furthermore, we found evidence for a functional overlap of selection mechanisms in memory and perception (Gazzaley & Nobre, 2012; Gazzaley, 2011; Awh et al., 2006), as encoding of peripheral tactile probe stimuli (indexed by the N140) was biased in favor of events that shared spatial properties with the retrospectively cued sample. The N140 to test stimuli was insensitive to spatial congruency. Hence, these results suggest that selection in tactile STM triggers transient shifts of spatial attention.

Our findings support a close link between retrospective selection and covert spatial orienting. Although attention-based rehearsal is similarly known to lead to spatial attention effects (Theeuwes et al., 2009; Awh et al., 2000, 2006; Jha, 2002), maintenance of locations was not required here. Our results point in the direction that spatially specific biasing of neural activity is caused by a time-variant process triggered by the presentation of the retro-cue. We conclude that the role of spatial attention in retro-

spective selection is functionally dissociable from attention-based rehearsal of locations.

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