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Full manuscript title:

The N2cc component as an electrophysiological marker of space-based and feature-based attentional target selection processes in touch

Running head:

Selection of tactile locations and features

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Keywords

- Electroencephalography (EEG), event-related potentials (ERPs)
- Somatosensory processing
- Spatial attention
- Feature-based attention

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Abstract

An electrophysiological correlate of attentional target selection processes in touch (N2cc component) has recently been discovered in lateralized tactile working memory experiments. This tactile N2cc emerges at the same time as the visual N2pc component, but has a different modality-specific topography over central somatosensory areas. Here, we investigated links between N2cc components and the space-based versus feature-based attentional selection of task-relevant tactile stimuli. On each trial, a pair of tactile items was presented simultaneously to one finger on the left and right hand. Target stimuli were defined by their location (e.g., left index finger; Spatial Attention Task), by a non-spatial feature (continuous versus pulsed; Feature-based Attention Task), or by a combination of spatial and non-spatial features (Conjunction Task). Reliable N2cc components were observed in all three tasks. They emerged considerably earlier in the Spatial Attention Task than in the Feature-based Attention Task, suggesting that space-based selection mechanisms in touch operate faster than feature-guided mechanisms. The temporal pattern of N2cc components observed in the Conjunction Task revealed that space-based and feature-based attention both contributed to target selection, which was initially driven primarily by spatial location. Overall, these findings establish the N2cc component as a new electrophysiological marker of the selective attentional processing of task-relevant stimuli in touch.

Introduction

The sensory processing of stimuli in vision and in touch shows many similarities. In both modalities, sensory areas in each hemisphere process signals from the contralateral side of visual or somatosensory space, and these sensory areas include two-dimensional spatial maps where information is represented in retinotopic or somatotopic coordinates. Given these analogies, the question arises whether mechanisms of selective attention also operate in a qualitatively similar fashion in both modalities. In vision, the allocation of attention to currently task-relevant stimuli is associated with an increase of neural activity at particular locations within visual maps in extrastriate cortical areas (e.g., Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985). Similar attention-dependent activity modulations have also been observed in somatosensory cortex (e.g., Hsiao, O'Shaughnessy, & Johnson, 1993; Steinmetz et al., 2000). This is in line with the results of event-related potential (ERP) studies, which have revealed attentional modulations of early sensory-evoked ERP components both in vision (e.g., Eimer, 1994; Mangun & Hillyard, 1991) and touch (e.g., Eimer & Forster, 2003; Michie, 1984).

One central function of selective attention is to facilitate the ability to search for target objects in tasks where these objects are presented together with task-irrelevant distractors. In visual search tasks, observers have to find targets that are defined by specific features (such as color, shape) or feature conjunctions, and appear at unpredictable locations among multiple distractor objects (e.g., Treisman & Gelade, 1980). An electrophysiological marker of attentional selection of such visual search

targets is the N2pc component. The N2pc typically emerges between 180 and 200 ms post-stimulus at posterior electrodes contralateral to the side of candidate target objects in visual search displays (e.g., Eimer, 1996; Luck & Hillyard, 1994a, 1994b; Woodman & Luck, 1999), and is generated in extrastriate ventral visual cortex (Hopf et al., 2000). It is assumed to reflect the enhancement of neural responses for objects with target-matching features at specific locations within visual cortical maps (see Eimer, 2014, 2015, for further discussion). The N2pc component has been employed in many studies of visual attention and visual search (see Luck, 2012, for review). It is elicited in search tasks where targets are defined by a specific feature (such as color or shape; e.g., Luck & Hillyard, 1994a; Eimer & Grubert, 2014), and also during search for targets that are defined by feature conjunctions (e.g., Luck & Ford, 1998; Fuggetta, Pavone, Walsh, Kiss, & Eimer, 2006). N2pc amplitudes increases in size when the number of attended target objects increases (Drew & Vogel, 2008; Mazza & Caramazza, 2011), indicating that this component is associated with the allocation of attention to individual target objects.

If attentional processes in vision and touch operate in qualitatively similar ways, one could predict that the attentional selection of tactile target objects among distractors in somatosensory search tasks will be reflected by a lateralized tactile ERP component that emerges at approximately the same time as the visual N2pc, but shows a different modality-specific topography over somatosensory cortex. Initial evidence for the existence of such a somatosensory equivalent of the N2pc component was found in the context of a tactile working memory study from our lab (Katus, Grubert, & Eimer, 2015). Tactile sample stimuli were presented simultaneously to both hands, and participants

had to memorize samples on one task-relevant hand in order to compare them to a subsequent test stimulus set. Sample stimulus sets elicited an enhanced negativity contralateral to the task-relevant hand that emerged around 180 ms after stimulus onset and was maximal at lateral central electrodes over somatosensory areas. Similar to the visual N2pc component, which increases in amplitude with the number of attended objects (e.g., Mazza & Caramazza, 2011), this contralateral negativity was larger when observers encoded two as compared to just one tactile sample item on the task-relevant hand. This similarity to the N2pc, as well as the fact that this somatosensory component was elicited within the same post-stimulus time window, and showed an analogous topography over contralateral modality-specific sensory brain areas, led us to refer to this component as central-contralateral N2 (N2cc component). We suggested that analogous to its visual equivalent, it reflects the allocation of selective attention to task-relevant tactile stimuli that are accompanied by to-be-ignored tactile distractors.

There was however an important difference between the selection task used in this tactile working memory experiment (Katus et al., 2015) and typical visual search tasks. In our study, task-relevant tactile sample items were defined by their anatomical location (left versus right hand). In contrast, target objects in visual search appear among distractors at unpredictable spatial locations in the visual field, and are defined not by their position, but by other attributes such as their color, shape, or orientation. Given this difference between feature-guided and space-based attentional selection processes, it remains an open question whether the N2cc component observed during the encoding of tactile sample items is functionally equivalent to the N2pc found during the allocation of attention to objects with target-matching features in visual search tasks.

The goal of the present study was to clarify the links between N2cc components and the space-based versus feature-based attentional selection of task-relevant items in the somatosensory modality.

We measured lateralized tactile ERP components in three attentional selection tasks. In all three tasks, a pair of tactile stimuli was presented simultaneously to the left and right hand, either to the index or middle finger of each hand. These stimuli also differed with respect to a non-spatial feature (continuous vibration versus two pulses separated by a temporal gap). In the Spatial Attention Task, participants had to attend to one particular target location (e.g., left index finger), in order to report whether a tactile stimulus was presented to this location or not, irrespective of whether this stimulus was continuous or pulsed. Half of all trials were target-absent trials where the other location on the relevant hand (e.g., left middle finger) was stimulated. In this task, the selection of the tactile target stimulus was purely space-based. In the Feature-based Attention Task, either continuous or pulsed stimuli served as targets, and these targets were presented with equal probability to the index or middle finger of the left or right hand. Participants had to detect the feature-defined target and report whether this target was presented to the left or right hand. In the Conjunction Task, tactile targets were defined by a combination of spatial and non-spatial features (e.g., continuous stimuli delivered to the left index finger), and participants had to report the presence or absence of a target on each trial. On target-absent trials, tactile stimuli on the task-relevant hand could have only one or neither of the two target-defining attributes.

EEG was recorded during task performance, and ERPs were computed for electrodes contralateral and ipsilateral to the task-relevant hand, separately for the three

attention tasks. Because the goal of this study was to assess the N2cc as a new electrophysiological marker of attentional target selection in touch, we focused our analyses of ERP data on the post-stimulus latency range where this component was expected to be elicited. The presence of N2cc components was assessed within a 100 ms time window starting at 180 ms post-stimulus, where the N2cc was found to emerge in our previous study (Katus et al., 2015). Given that an N2cc was elicited in this study when spatial attention was directed to the left or right hand in order to encode tactile samples delivered to this hand into working memory, we expected to find reliable N2cc components in the Spatial Attention Task of the current experiment. The presence of N2ccs in this task could reflect the spatially global attentional selection of all tactile events delivered to the task-relevant hand, or a more spatially specific selection of attended locations within a specific hand. In the former case, N2cc components of similar size should be triggered in the Spatial Attention Task on trials where the to-be-attended finger on the relevant hand was stimulated, and on target-absent trials where a tactile stimulus was presented to the other finger of the same hand. Alternatively, if the N2cc reflects the more fine-grained allocation of spatial attention to task-relevant fingers, this component should be much larger on target-present trials, and possibly entirely absent on target-absent trials.

A critical question addressed in the present study was whether an N2cc is only triggered during the space-based selection of task-relevant tactile stimuli, or also when these target stimuli are defined by non-spatial attributes, as is the case for the visual N2pc component. If an N2cc is generated during feature-guided attentional selection processes in touch, it should be elicited contralateral to tactile target objects in the

Feature-based Attention Task. Any difference in the speed of space-based versus feature-based tactile target selection should be reflected by target N2cc onset latency differences between the Spatial and Feature-based Attention Tasks.

In the Conjunction Task, we assessed the roles of spatial and feature-based attention when tactile target items were defined by a combination of spatial and non-spatial attributes. One possibility is that the attentional selection of tactile stimuli is determined exclusively by spatial attention under these conditions (see Hillyard & Anllo-Vento, 1998, for ERP results suggesting such a dominance of space-based over feature based selectivity in visual attention). In this case, N2cc components measured in the Conjunction Task should show an identical pattern as in the Spatial Attention Task, regardless of whether tactile stimuli at attended locations also possess the non-spatial target-defining feature (continuous or pulsed). Alternatively, space-based and feature-based attention may both contribute to the selection of tactile stimuli in the Conjunction Task. One possibility is that these two types of attentional control processes operate in an interactive fashion, so that attention is allocated primarily or exclusively to tactile target stimuli that match both target-defining attributes. In this case, clear N2cc components should be triggered by these target items, while N2ccs to partially target-matching tactile stimuli should be strongly attenuated or entirely absent. It is also possible that space-based and feature-based attention operate independently and in parallel. This should be reflected by N2cc components for tactile stimuli at attended locations and for stimuli with the attended non-spatial attribute, without an interaction between spatial and feature-based attention.

Methods

Participants

16 neurologically unimpaired participants were tested. All gave informed written consent prior to testing. One participant was excluded from analyses due to low performance (> 30% error rate in the Feature Task) and another due to excessive EEG artifacts affecting more than 40% of all trials. Fourteen participants remained in the sample (age range: 24-45 years, average age: 30 years, 5 female, 13 right-handed). The experiment was conducted in accordance with the Declaration of Helsinki, and was approved by the Psychology Ethics Committee, Birkbeck, University of London.

Apparatus and stimulation procedures

Tactile stimuli were delivered by four mechanical stimulators (Dancer Design, St. Helens, UK) that were attached to the left and right hands' distal phalanges of the index and middle fingers (see Figure 1). The stimulators were driven by custom-built amplifiers, controlled by MATLAB routines (The MathWorks, Natick, USA) using the computer's sound card (M-Audio, Delta 1010LT). The experiments took place in a dimly lit recording chamber. The distance between the left and the right hand of the participant was approximately 30 cm, and both hands were covered from sight. Headphones played continuous pink noise to mask any sounds produced by tactile stimulation. On each trial, a pair of tactile stimuli was presented for 300 ms. One stimulus was

presented to the index or middle finger of the left hand, the other simultaneously to the index or middle finger of the right hand. Stimuli were either continuous or pulsed. The continuous stimulus was a 100-Hz sinusoid with an intensity of 0.30N. The pulsed stimulus consisted of two 30 ms long sinusoids (frequency: 100 Hz, intensity: 0.37N¹) that were separated by an interval of 240 ms. The interval between the offset of tactile stimuli on the preceding trial and the onset of the tactile stimulus pair on the next trial was jittered (ranging from 1640 ms to 1960 ms; mean: 1810 ms). A vocal response (“a” or “e”) was required on each trial. These responses were recorded using a headset microphone in the 1500 ms period following stimulus onset. The onset and correctness of each vocal response was determined on-line, using custom-written Matlab routines. These classifications were manually rechecked offline after the experiment. Participants completed three attention tasks (as described below), with task order randomized across participants. Prior to the start of the first experimental block for each task, a brief practice block containing 15-20 training trials was run. Task instructions were provided by the experimenter prior to the start of the training phase, and were additionally displayed on the monitor before each experimental block. The monitor also provided feedback on performance (accuracy, reaction times) after each block.

¹ A stimulus consisting of a few short pulses inevitably feels less intense than a continuous vibration if both types of stimuli are presented with the same physical intensity. Hence, we presented the pulsed stimulus with the maximum intensity our factors could provide, and reduced the intensity of the continuous stimulus to match it with the felt intensity of the sensation elicited by the pulsed stimulus.

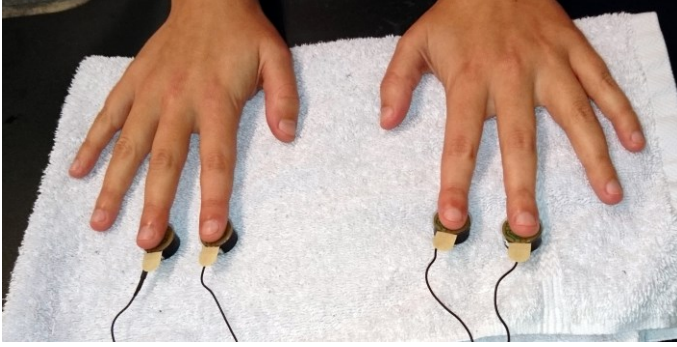


Figure 1. Stimulation hardware: Four tactile stimulators were attached to the fingertips of the index and middle fingers of the left and right hands. Note that the hands were covered from sight during the experiment.

Spatial Attention Task

A continuous tactile stimulus was delivered to the left hand and a pulsed stimulus to the right hand, or vice versa, and this varied randomly across trials. Stimulus location (index or middle finger) was determined randomly and independently for the left and right hands. Participants were instructed to attend to one finger on one hand, and to report on each trial whether this attended finger was stimulated (by saying “a”; target-present trials) or not (by saying “e”; target-absent trials). The attended finger received a stimulus on 50% of all trials. Stimulus type (continuous or pulsed) was irrelevant for this task. Four experimental blocks with 48 trials each were run, resulting in 96 target-present and 96 target-absent trials. The to-be-attended finger changed after every block. Seven participants attended to the left index, left middle, right middle, and right index finger, in blocks 1, 2, 3, and 4, respectively. For the other seven participants, this order was reversed.

Feature-based Attention Task

Stimulus presentation procedures were identical to the Spatial Attention Task, but task instructions were different. In contrast to the Spatial Attention Task, but analogous to typical visual search tasks, target location was unpredictable, and targets were defined by a non-spatial attribute. Participants were instructed to attend either to the continuous or to the pulsed stimulus, and to report (by saying “a” or “e”) whether this target stimulus was presented to the index/middle finger of the left hand or to the index/middle finger of the right hand. Two blocks with 48 trials were run, resulting in a total of 96 target-present trials. In contrast to the Spatial Attention Task, there were no target-absent trials. The non-spatial target attribute (continuous or pulsed) for the first block was randomly selected for each participant, and was changed for the second block.

Conjunction Task

Targets were now defined by a combination of spatial location (e.g., index finger of the right hand) and a non-spatial stimulus attribute (continuous or pulsed). The stimulus delivered to the task-relevant hand was either continuous or pulsed and was presented either to the attended or unattended finger, with equal probability. As a result, there were 25% target-present trials where the stimulus delivered to the relevant hand matched both target-defining attributes (e.g., index finger/pulsed). On the remaining target-absent trials, the stimulus on the task-relevant hand matched only the attended location (e.g., index finger/continuous), only the attended non-spatial feature (e.g., middle finger/pulsed) or neither of these attributes (e.g., middle finger/continuous), each

with equal probability (25% of all trials). The tactile stimulus on the other task-irrelevant hand was equally likely to be presented to the index or middle finger. Because target location matches could by definition never occur on this task-irrelevant hand, non-spatial target feature matches were also absent for this hand, as all tactile items presented to this hand matched the currently unattended non-spatial attribute (e.g., continuous in blocks where targets were pulsed). Participants reported the presence or absence of the conjunctively defined target by saying “a” or “e”, respectively. They completed 8 blocks with 48 trials each, resulting in 96 trials for each of the four different trial types (target-present; target-absent with a spatially matching, feature-matching or non-matching tactile stimulus on the task-relevant hand). The non-spatial target feature (continuous or pulsed) in the first block was randomly determined for each participant. It then remained constant for four successive blocks, and changed for blocks 5-8. The target-defining location in the first block was the middle finger of the left or right hand (randomly determined for each participant). It changed after each block, either from left to right or from right to left (analogous to the Spatial Attention Task). The same sequence of target-defining locations was then repeated in blocks 5-8, where they were combined with the other non-spatial target attribute.

EEG data acquisition and pre-processing

EEG data, sampled at 500 Hz using a BrainVision amplifier, were DC-recorded from 32 Ag/AgCl active electrodes at standard locations of the extended 10-20 system. Two electrodes at the eyes' outer canthi monitored horizontal eye movements (horizontal electrooculogram, HEOG). Continuous EEG data were referenced to the left

mastoid during recording, and re-referenced to the arithmetic mean of both mastoids for data pre-processing. Data were offline submitted to a 20 Hz low-pass filter (Blackman window, filter order 3000). EEG epochs were generated for a 500 ms period after stimulus onset, and amplitude values were computed relative to the mean of a 100 ms pre-stimulus baseline.

Trials with saccades were rejected using a step function that ran on the bipolarized HEOG (step width 200 ms, threshold 30 μV). Trials in which difference values for corresponding left- minus right-hemispheric electrodes exceeded a fixed threshold of $\pm 80 \mu\text{V}$ (for any electrode pair) were also rejecting, resulting in an exclusion of 3.3% of all epochs. *Independent Component Analysis* (ICA) (Delorme, Sejnowski, & Makeig, 2007) was subsequently used to correct for EEG artefacts resulting from eye blinks, and residual traces of horizontal eye movements that had not been detected by the step function. Statistical analyses were based on correct and incorrect trials, as the exclusion of incorrect trials did not change the pattern of results.

Analyses of ERPs and behavioral performance

The N2cc was measured on the basis of tactile ERPs recorded over somatosensory cortex (electrodes C3 and C4; cf. Katus et al., 2015) contralateral and ipsilateral to the currently task-relevant hand. N2cc components were always defined as an enhanced negativity at electrodes contralateral to the anatomical side of the attended hand in the Spatial Attention and Conjunction Tasks (regardless of whether the index or middle finger of this hand was attended in a given block), and contralateral to the hand that received the attended non-spatial attribute in the Feature-based

Attention Task. N2cc mean amplitudes were computed within a 180-280 ms post-stimulus time window. The choice of this time window was informed by our previous study that described the N2cc for the first time (Katus et al., 2015) where this component emerged around 180 ms after stimulus onset. Because the N2cc in the Feature-based Attention Task was delayed (see below), an additional analysis was conducted within a later time window (240-320 ms post-stimulus) that was informed by determining the onset latency of the contralateral negativity in this task. Data were analyzed with repeated-measures ANOVAs and paired t-tests. Bayesian t-tests (Rouder, Speckman, Sun, Morey, & Iverson, 2009) and the software Jasp (JASP team, 2016) were used to calculate Bayes factors for each main effect / interaction in our statistical designs.

In addition to N2cc components, accuracy and reaction times (RTs) were also measured in the three tasks. Paired t-tests were used to compare performance between spatial match versus mismatch trials in the Spatial Attention Task. Behavioral data in the Conjunction Task were analyzed with repeated-measures ANOVAs with the factors Spatial Attention and Feature-based Attention. Because the Feature-based Attention Task only involved one condition (there was a target on every trial), only mean RT and accuracy are reported for this task.

Results

Spatial Attention Task

Performance

Participants were faster to report the presence of a target at the attended location than the absence of a target at this location (643 ms vs. 688 ms, $t(13) = 4.442$, $p < 0.001$, $d = 1.187$, $BF_{10} = 55.601$). Participants' accuracy was close to ceiling on the location task (97.7% correct), and did not differ between target-present and target-absent trials ($t(13) = 0.840$, $p = 0.416$, $d = 0.225$, $BF_{01} = 2.734$).

N2cc component

ERP mean amplitudes at electrodes C3/C4 contralateral and ipsilateral to the task-relevant hand in the 180-280 ms post-stimulus interval were analyzed in a repeated measures ANOVA with the factors Laterality (electrode contralateral vs. ipsilateral to the task-relevant hand) and Spatial Attention (stimulus at attended vs. unattended finger on the task-relevant hand). A main effect of Laterality ($F(1, 13) = 40.710$, $p < 10^{-4}$, $\eta_p^2 = 0.758$, $BF_{10} > 10^3$) confirmed the presence of an N2cc component in this task. Importantly, the N2cc was larger on target-present trials where the attended finger on the task-relevant hand was stimulated than on target-absent trials where the other unattended finger on this hand was stimulated, as reflected by an interaction between Laterality and Spatial Attention ($F(1, 13) = 15.167$, $p = 0.002$, $\eta_p^2 = 0.538$, $BF_{10} = 23.250$); see Figure 2A. Follow-up t-tests comparing contralateral and ipsilateral ERP amplitudes confirmed that a reliable N2cc component was present not only on target-present trials ($t(13) = 6.459$, $p < 10^{-4}$, $d = 1.726$, $BF_{10} > 10^3$), but also on target-absent trials ($t(13) = 3.916$, $p = 0.002$, $d = 1.047$, $BF_{10} = 24.072$).

Feature-based Attention Task

Performance

In this task, participants reported on each trial whether the target stimulus had been delivered to the left or right hand. Mean RT was 873 ms, and response accuracy was 91.5%. A comparison of performance between this task and target-present trials in the Spatial Attention Task showed that RTs were reliably slower ($t(13) = 7.645$, $p < 10^{-5}$, $d = 2.043$, $BF_{10} > 10^3$) and errors more frequent ($t(13) = 4.052$, $p = 0.001$, $d = 1.083$, $BF_{10} = 29.933$) in the Feature-based Attention Task.

N2cc components

As can be seen in Figure 2B, the onset of the negativity contralateral to the hand where the target stimulus was delivered was delayed in this task relative to the Spatial Attention Task. As a consequence of this delay, there was no reliable N2cc during the 180-280 ms post-stimulus time window, as the contralateral-ipsilateral difference only approached significance ($t(13) = 1.864$, $p = 0.085$, $d = 0.498$, $BF_{10} = 1.053$). To determine the onset of the contralateral negativity in the Feature-based Attention Task and to assess whether it was reliably delayed relative to the Spatial Attention Task, we calculated and compared the onset latencies elicited on target-present trials in both tasks, using the jackknife-based method described by Miller, Patterson, & Ulrich (1998).² This comparison confirmed that a contralateral negativity emerged significantly

² For this analysis, contralateral minus ipsilateral difference waveforms were computed for each participant, and fourteen grand-average difference waves were generated, each excluding one

later in the Feature-based Attention Task (260 ms post-stimulus, as compared to 166 ms in the Spatial Attention Task; $t(13) = 5.783$, $p < 10^{-4}$, $d = 1.546$, $BF_{10} = 428.068$). Informed by this onset latency estimate for the Feature-based Attention Task, we computed ERP mean amplitudes within a later 240-320 ms post-stimulus interval. For this time window, reliable contralateral-ipsilateral differences were indeed found ($t(13) = 3.254$, $p = 0.006$, $d = 0.870$, $BF_{10} = 8.322$); see Figure 2B.

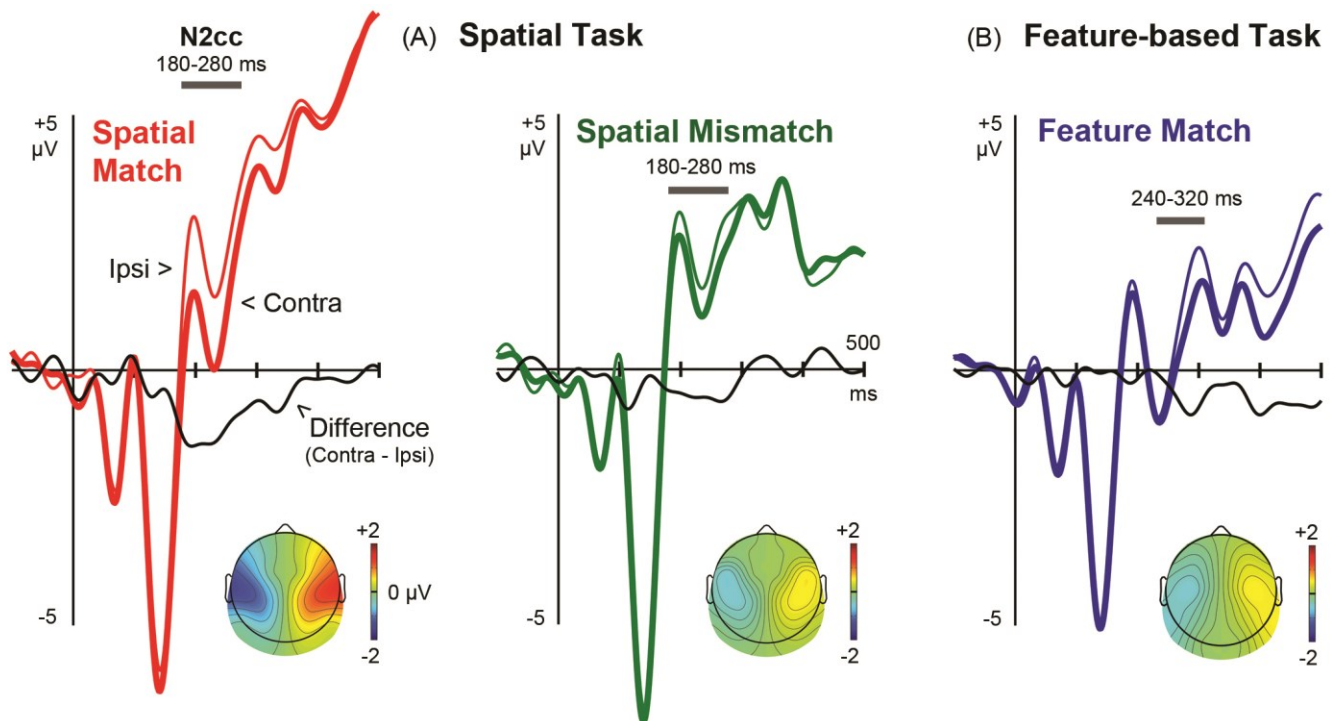


Figure 2. (A) Spatial Attention Task: ERPs elicited by tactile stimuli at electrodes C3/C4 contralateral (thick lines) and ipsilateral (thin lines) to the task-relevant hand; black lines

different participant from the original sample. N2cc onset latency was defined as the point in time when each subsample difference wave exceeded a relative onset criterion of 50% of peak N2cc amplitude within a pre-defined broad time window ranging from 120 ms to 300 ms post-stimulus. N2cc onset latency differences between task conditions were assessed with paired t-tests, with t-values corrected according to the formulas described by Miller et al. (1998).

indicate difference values of contralateral minus ipsilateral ERPs. On target-present (spatial match) trials, the tactile stimulus was presented to the attended finger of the relevant hand. On target-absent (spatial mismatch) trials, it was presented to the unattended finger on this hand. (B) Feature-based Attention Task: ERPs contralateral and ipsilateral to the side of the tactile stimulus with the attended non-spatial stimulus feature (continuous or pulsed). The topographical maps show the spline-interpolated scalp distribution of N2cc components during the 180-280 ms post-stimulus time window in the Spatial Attention Task, and during the 240-320 ms window in the Feature-based Attention Task. These maps were based on contralateral-ipsilateral difference waveforms, with electrode coordinates flipped over the midline for trials/blocks where the left hand was relevant (Spatial Attention Task), or received the stimulus with the attended feature (Feature-based Attention Task). As a consequence, a negative potential over the left hemisphere indicates the presence of a contralateral N2cc in these maps.

Conjunction Task

Performance

RTs and error rates were analyzed separately in ANOVAs with the factors Spatial Attention (stimulus at attended vs. unattended finger on the task-relevant hand) and Feature-based Attention (stimulus with the attended vs. unattended feature on the task-relevant hand). RTs were faster on target-present trials and in trials where the stimulus on the task-relevant hand matched neither the target-defining spatial location nor its

non-spatial feature (648 ms and 665 ms) relative to target-absent trials where the stimulus had one target-matching and one target-nonmatching attribute (688 ms vs. 680 ms for feature-match vs. location-match trials, respectively). This difference was reflected by a significant interaction between Spatial and Feature-based Attention $F(1, 13) = 20.153, p = 0.001, \eta_p^2 = 0.608, BF_{10} = 59.899$. There were no main effects of Spatial Attention ($F(1, 13) = 0.179, p = 0.679, \eta_p^2 = 0.014, BF_{01} = 3.424$) or Feature-based Attention ($F(1, 13) = 2.023, p = 0.178, \eta_p^2 = 0.135, BF_{10} = 1.614$) for RTs. Accuracy was generally high (98.8%). A main effect of Spatial Attention ($F(1, 13) = 10.719, p = 0.006, \eta_p^2 = 0.452, BF_{10} = 8.599$) was due to the fact that performance was slightly more accurate on trials where the attended finger on the task-relevant hand was stimulated (99.4% correct vs. 98.1% when the other unattended finger was stimulated). There was no reliable effect of Feature-based attention ($F(1, 13) = 3.521, p = 0.083, \eta_p^2 = 0.213, BF_{10} = 1.070$) for accuracy, and no significant interaction between both factors ($F(1, 13) = 0.774, p = 0.395, \eta_p^2 = 0.056, BF_{01} = 2.658$).

N2cc components

N2cc components in the 180-280 ms post-stimulus time window were analyzed with the factors Laterality, Spatial Attention, and Feature-based Attention. A significant effect of Laterality ($F(1, 13) = 25.248, p < 0.001, \eta_p^2 = 0.660, BF_{10} = 137.735$) confirmed the presence of N2cc components in the Conjunction Task. As shown in Figure 3, N2cc components were much larger on target-present trials where the tactile stimuli on the task-relevant hand was delivered to the attended finger and matched the target-defining non-spatial attribute relative to the other three types of trials. This difference was

reflected by interactions between Laterality and Spatial Attention ($F(1, 13) = 6.720$, $p = 0.022$, $\eta_p^2 = 0.341$, $BF_{10} = 2.964$), Laterality and Feature-based Attention ($F(1, 13) = 9.683$, $p = 0.008$, $\eta_p^2 = 0.427$, $BF_{10} = 6.644$), and a reliable three-way interaction ($F(1, 13) = 9.511$, $p = 0.009$, $\eta_p^2 = 0.423$, $BF_{10} = 6.358$)

To further examine these interactions, we conducted separate ANOVAs for spatial match trials where a tactile stimulus was presented to the attended finger on the task-relevant hand (Figure 3, top panel) and spatial mismatch trials where the unattended finger on this hand was stimulated (Figure 3, bottom panel). On spatial match trials, a main effect of Laterality ($F(1, 13) = 44.308$, $p < 10^{-4}$, $\eta_p^2 = 0.773$, $BF_{10} > 10^3$) reflected the presence of N2cc components. Importantly, there was a Laterality x Feature-based Attention interaction ($F(1, 13) = 11.138$, $p = 0.005$, $\eta_p^2 = 0.461$, $BF_{10} = 9.514$), confirming that the N2cc to tactile stimuli at the attended finger was larger on target-present trials where these stimuli also matched the target-defining non-spatial attribute. However, follow-up analyses comparing contralateral and ipsilateral ERPs showed that a reliable N2cc component was not only triggered on feature match trials ($t(13) = 6.324$, $p < 10^{-4}$, $d = 1.690$, $BF_{10} = 928.768$) but also when the stimulus presented to the attended finger did not match the non-spatial target attribute ($t(13) = 2.403$, $p = 0.032$, $d = 0.642$, $BF_{10} = 2.234$).

On spatial mismatch trials, a main effect of Laterality ($F(1, 13) = 4.972$, $p = 0.044$, $\eta_p^2 = 0.277$, $BF_{10} = 1.737$) suggested that a small N2cc component was also elicited by stimuli delivered to the unattended finger of the task-relevant hand, analogous to what had been observed in the Spatial Attention Task (Figure 2A). There was no interaction between Laterality and Feature-based Attention ($F(1, 13) = 0.274$, $p = 0.610$, $\eta_p^2 =$

0.021, $BF_{01} = 3.286$), which indicates that this residual N2cc was not modulated by the presence or absence of the non-spatial target attribute.

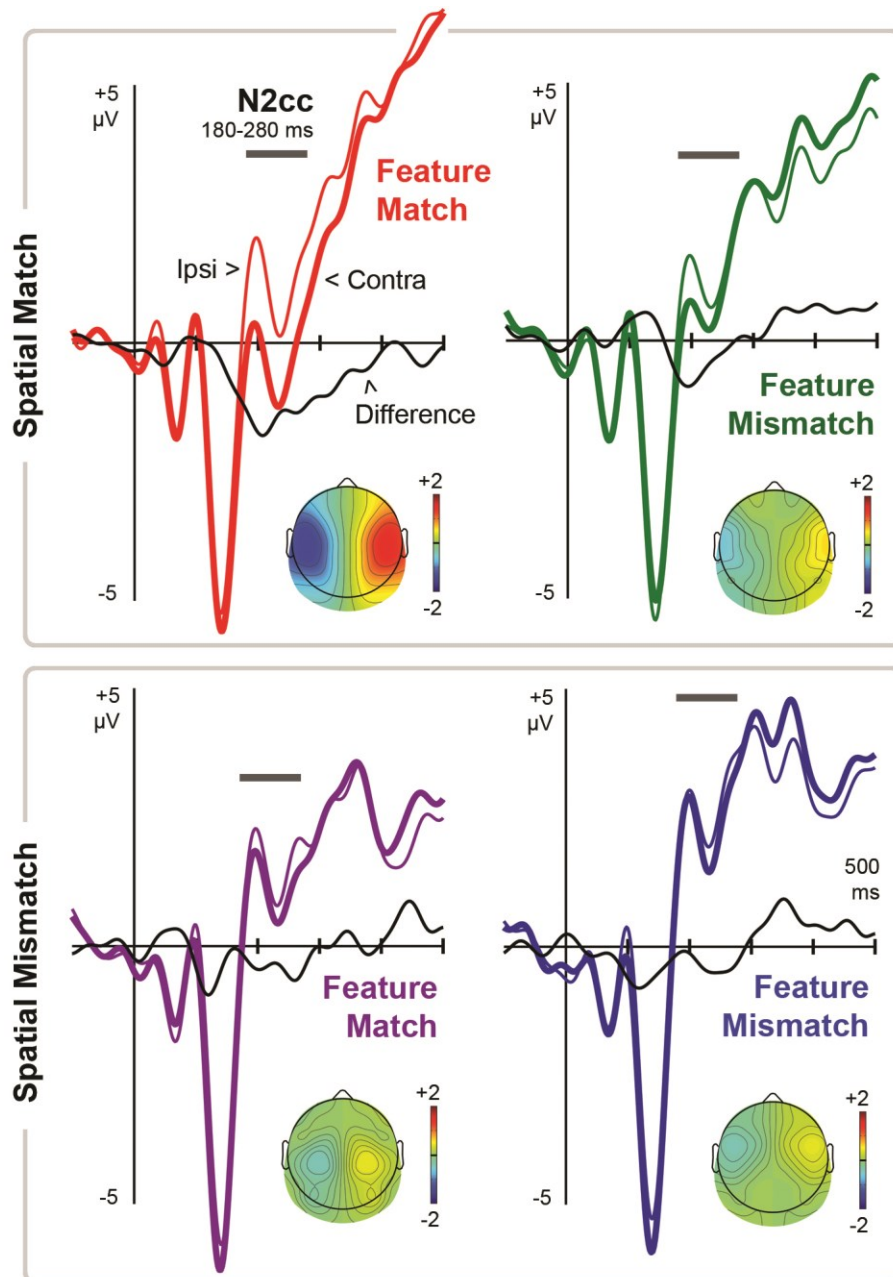


Figure 3. ERPs elicited at electrodes C3/4 contralateral and ipsilateral to the currently task-relevant hand (thick vs. thin lines) in the four conditions of the Conjunction Task;

black lines represent contra-/ipsilateral difference values. On Spatial Match trials (top panels), a tactile stimulus was presented to the attended finger of the task-relevant hand. On Spatial Mismatch trials (bottom panels), it was presented to the other unattended finger on this hand. On Feature Match trials (left panels), the tactile stimuli presented to the task-relevant hand matched the target-defining feature. On Feature Mismatch trials (right panels), it matched the other currently task-irrelevant non-spatial feature. Topographic maps illustrate the scalp distribution of N2cc components during the 180-280 ms post-stimulus time window for all four conditions.

Discussion

We recorded somatosensory ERPs to pairs of tactile stimuli presented simultaneously to one finger of each hand in three attentional selection tasks where tactile target objects were either defined by their location (Spatial Attention Task), by a non-spatial attribute (Feature-based Attention Task), or by a combination of spatial and non-spatial features (Conjunction Task). ERPs were measured over somatosensory cortex contralateral and ipsilateral to the currently task-relevant tactile stimulus, and tactile N2cc components were computed for all three tasks, in order to assess whether this component is an ERP marker for space-based and/or feature-based attentional target selection processes in touch.

In the Spatial Attention Task, clear N2cc components were elicited contralateral to the currently task-relevant hand, demonstrating that the N2cc reflects the allocation of tactile attention to spatially defined target items. This observation confirms the result of

a previous experiment (Katus et al., 2015) where N2cc components were found in a task where tactile sample stimuli presented to a task-relevant hand had to be encoded into working memory, while stimuli delivered concurrently to the other irrelevant hand could be ignored. Importantly, N2cc components triggered in the current Spatial Attention Task were much larger on target-present trials where a tactile stimulus was presented to the attended finger of the task-relevant hand than on target-absent trials where a different finger on this hand was stimulated. This difference shows that N2cc components do not exclusively reflect the spatially global allocation of tactile attention to one hand versus the other, but a more precise attentional selection process that can be tuned to particular locations (individual fingers) within one hand. This result converges with previous ERP evidence for the within-hand spatial selectivity of tactile attention reported in experiments where only a single tactile stimulus was presented on each trial (Eimer & Forster, 2003). Notably, in the present study, we found attenuated, but still reliable, N2cc components in the Spatial Attention Task on trials where the unattended finger on the task-relevant hand was stimulated. This shows that the tuning of space-based tactile selectivity was not perfectly accurate in this task, as to-be-ignored locations on the relevant hand were not entirely excluded from attentional processing.

In the Feature-based Attention Task, tactile targets and nontargets were defined by a non-spatial attribute (continuous vibration versus two pulses separated by a gap) and targets appeared unpredictably at any of four possible locations on each trial. Here, no reliable negativity was elicited contralateral to target objects during our standard 180-280 ms post-stimulus analysis window. Additional analyses revealed that this effect was reliably delayed relative to the Spatial Attention Task, and was significant within a later

240-320 ms time window. This raises the question whether the contralateral negativity observed in the Feature-based Attention Task can be interpreted as an N2cc component. In this task, the discrimination between continuous and pulsed tactile stimuli only became possible from 30 ms after stimulus onset, following the offset of the first pulse involved in the pulsed stimulus category. In contrast, the location of tactile stimuli that defined target items in the Spatial Attention Task on any given trial was accessible from the moment when these stimuli were presented.³ As a result, any allocation of attention to tactile targets should have been triggered later in the Feature-based Attention task than in the Spatial Attention Task, resulting in a delay of corresponding N2cc components. In this context, the observation that this delay was substantial (about 90 ms) could suggest that feature-guided attentional selection processes in touch are generally slower than space-based selection mechanisms.

When considering whether the contralateral negativity observed in the Feature-based Attention Task represents a genuine N2cc component indicative of attentional target selection, it is notable that two other recent ERP investigations of tactile attention (Ambron, Mas-Casadesus, & Gherri, 2018; Forster, Tziraki, & Jones, 2016) also reported enhanced negativities contralateral to tactile target stimuli in tasks where these

³ The delay of the contralateral negativity in the Feature-based Attention Task could in principle reflect a failure of participants to consistently implement the instructed target/nontarget assignments in this task. Because each trial always contained a continuous and a pulsed tactile stimulus on opposite sides, participants could have decided to attend the tactile stimulus feature that was nominally the nontarget, while simultaneously reversing the instructed left/right response mapping. Some participants may have adopted such a strategy specifically in the second block of this task, where target and nontarget attributes were reversed. In this case, N2cc components of opposite polarity should have been elicited in block 2. To assess this, we calculated contralateral-ipsilateral differences within the 240-320 ms post-stimulus time window separately for blocks 1 and 2, and found no evidence for such polarity reversals. In fact, contralateral negativities were numerically, but not statistically, larger in block 2 (-0.958 μ V versus -0.845 μ V; $t(13) = 0.197$, $p = 0.847$, $d = 0.053$, $BF_{01} = 3.641$), indicating that participants selected target items in line with task instructions in both blocks.

targets were defined by a non-spatial attribute (tap versus buzz). The fact that these effects emerged early (at about 140 ms post-stimulus) suggests that they may have been associated with a rapid bottom-up capture of tactile attention that is driven by the perceptual salience of target items, in particular under conditions where these targets were feature singletons (Forster et al., 2016). However, Ambron et al. (2018) also reported a second contralateral negativity between 230 and 310 ms after stimulus onset, which was sensitive to the critical attentional manipulation in their task (target-distractor distance), and may be equivalent to the delayed contralateral negativity in the Feature-based Attention Task here. Overall, while it is plausible to assume that this effect reflects an N2cc component that is elicited during the allocation of attention to feature-defined tactile targets, this conclusion remains tentative at present. It needs to be confirmed in future tactile search studies where different types of target-defining attributes are compared.

The Conjunction Task was designed to assess the roles of spatial and feature-based tactile attention under conditions where tactile targets are defined by a combination of spatial and non-spatial attributes. Previous ERP results from tactile attention tasks where a single stimulus was presented on each trial (Forster & Eimer, 2004) have suggested that spatial and non-spatial attention modulate somatosensory processing in parallel and independently. In line with this interpretation, the N2cc elicited in the Conjunction Task on spatial match trials was larger for target items than for nontargets that were presented to the same attended location but lacked the target-defining non-spatial feature. This demonstrates that attentional selectivity was not controlled in an exclusively space-based fashion in this task, but was modulated by the

presence versus absence of the other non-spatial target feature. It is notable that the N2cc amplitude difference between targets and feature-mismatching nontargets on spatial match trials were apparent from around 200 ms post-stimulus (Figure 3), indicating that feature-guided attention already affected tactile processing at this relatively early stage. In contrast, a reliable contralateral negativity was only found from about 260 ms onwards in the Feature-based Attention Task, potentially suggesting a delayed onset of feature-guided attentional facilitations of somatosensory processing (see above). One possibility to account for this apparent discrepancy is to assume that the N2cc amplitude difference between targets and feature-mismatching nontargets on spatial match trials does not reflect an increased attentional bias for targets but instead a reduced bias for nontargets. Attention may be de-allocated rapidly from items that are presented to the task-relevant location but lack the target-defining non-spatial feature, and this could result in a reduction of N2cc amplitudes relative to target items, for which attentional facilitation remains present for a longer period. Finally, tactile stimuli presented to the task-irrelevant finger of the relevant hand elicited a small but significant N2cc component in the Conjunction Task. This mirrors the N2cc results in the Spatial Attention Task, and is indicative of limitations in the tuning of tactile spatial attention to task-relevant fingers only.

In summary, the results of the present study establish the recently discovered N2cc component as an electrophysiological marker of attentional selection processes in somatosensory search tasks where task-relevant tactile stimuli are presented simultaneously with tactile distractors. This component is sensitive to space-based and feature-based selection mechanisms in touch, and can track the time course of these

selection processes in real-time. Analogous to the well-known visual N2pc component that is elicited by target objects in visual search displays (Eimer, 1996; Luck & Hillyard, 1994a,b), the N2cc component shows a contralateral scalp topography that is centred over modality-specific somatosensory areas, and is triggered at approximately the same post-stimulus latency as the N2pc. Like the N2pc, which emerges both during visual search for specific target-defining features and during search for feature conjunctions (e.g., Luck & Ford, 1998), the N2cc manifests not only when observers have to detect one specific target feature or location, but also when tactile targets are defined by a combination of spatial and non-spatial attributes. These similarities suggest that N2pc and N2cc components may reflect analogous attentional selection mechanisms. We propose that both components are generated within modality-specific perceptual areas where the location of visual or somatosensory stimuli is represented in two-dimensional retinotopic or somatotopic maps. These components emerge during the spatially selective attentional enhancement of sensory processing at locations within these maps where currently task-relevant visual or tactile stimuli are represented. In other words, these two components may be interpreted as electrophysiological markers for functionally similar top-down controlled attentional allocation processes at relatively early sensory-perceptual stages of visual or somatosensory processing.

While the current results are consistent with this hypothesis that the N2pc and N2cc components reflect analogous attentional target selection processes in vision and touch, further research on the properties of the tactile N2cc is needed to confirm this interpretation. For example, N2pc components are triggered in response to perceptually salient but task-irrelevant visual popout stimuli, although N2pc amplitudes are increased

when these stimuli are targets (Luck & Hillyard, 1994a). It will have to be determined whether this is also the case for the N2cc. The onset latency of target N2pc components is delayed in conjunction search tasks when the discrimination between targets and distractors is difficult (e.g., Fuggetta et al., 2006), and it has to be tested whether tactile N2cc components show an analogous sensitivity to target-nontarget similarity. Overall, the current study has demonstrated that a lateralized N2cc component is reliably elicited during the attentional selection of tactile target stimuli that are presented together with tactile distractors in somatosensory versions of visual search tasks. These initial observations open the way for further investigations of the question whether this tactile N2cc component is exactly analogous to the visual N2pc, and thus of functional similarities in the way that top-down attention affects the activation states of sensory representations in these two modalities.

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