No Evidence for a Role of Spatially Modulated α -Band Activity in Tactile Remapping and Short-Latency, Overt Orienting Behavior

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Oscillatory α -band activity is commonly associated with spatial attention and multisensory prioritization. It has also been suggested to reflect the automatic transformation of tactile stimuli from a skin-based, somatotopic reference frame into an external one. Previous research has not convincingly separated these two possible roles of α -band activity. Previous experimental paradigms have used artificially long delays between tactile stimuli and behavioral responses to aid relating oscillatory activity to these different events. However, this strategy potentially blurs the temporal relationship of α -band activity relative to behavioral indicators of tactile-spatial transformations. Here, we assessed α -band modulation with massive univariate deconvolution, an analysis approach that disentangles brain signals overlapping in time and space. Thirty-one male and female human participants performed a delay-free, visual search task in which saccade behavior was unrestricted. A tactile cue to uncrossed or crossed hands was either informative or uninformative about visual target location. α -Band suppression following tactile stimulation was lateralized relative to the stimulated hand over central-parietal electrodes but relative to its external location over parieto-occipital electrodes. α -Band suppression reflected external touch location only after informative cues, suggesting that posterior α -band lateralization does not index automatic tactile transformation. Moreover, α -band suppression occurred at the time of, or after, the production of the saccades guided by tactile stimulation. These findings challenge the idea that α -band activity is directly involved in tactile-spatial transformation and suggest instead that it reflects delayed, supramodal processes related to attentional reorienting.

Key words: α -band activity; EEG; free viewing; tactile remapping; visual search

Significance Statement

Localizing a touch in space requires integrating somatosensory information about skin location and proprioceptive or visual information about posture. The automatic remapping between skin-based tactile information to a location in external space has been proposed to rely on the modulation of oscillatory brain activity in the α -band range, across the multiple cortical areas that are involved in tactile, multisensory, and spatial processing. We report two findings that are inconsistent with this view. First, α -band activity reflected the remapped stimulus location only when touch was task relevant. Second, α -band modulation occurred too late to account for spatially directed behavioral responses and, thus, only after remapping must have taken place. These characteristics contradict the idea that α -band directly reflects automatic tactile remapping processes.

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Introduction

Oscillatory α -band activity is modulated when human participants expect, process, or plan movements toward, visual, auditory, or tactile stimulation (Schürmann and Başar, 2001; Foxe and Snyder, 2011; Buchholz et al., 2013). α -Band activity is usually suppressed contralateral to the attended or stimulated side of space, but can also be enhanced ipsilaterally, in either case leading to hemispheric α -band lateralization. Because spatially specific α -band modulation is common across modalities and tasks,

it has been suggested to reflect a supramodal spatial control mechanism (Klimesch et al., 2007; Jensen and Mazaheri, 2010).

However, for touch, it is not immediately clear how preparing for, or processing, a tactile stimulus should translate to α -band lateralization. The native reference frame of touch is skin-based, or somatotopic, that is, based on the body's anatomy. Somatotopic coding differs from visual or, more generally, external coding because body parts frequently change position. Touch location in external space depends on limb posture; for instance, when the right hand crosses the midline, it is located in left external space. Somatotopic and external effects both predict α -band modulation in the same hemisphere when a touched limb (e.g., a hand) is uncrossed. In contrast, when the limb is crossed, the two coding schemes make opposite predictions about which hemisphere should exhibit α -band suppression. α -Band modulation has been shown to reflect both somatotopic and external coding. Over primary somatosensory areas, α -band modulation depends on which hand is attended or stimulated, independent of posture (Buchholz et al., 2011, 2013; Schubert et al., 2015, 2019). In contrast, over occipito-parietal areas, α -band suppression depends on posture, indicating coding in external coordinates (Schubert et al., 2015, 2019).

Because occipito-parietal α -band modulation depends on the external location of touch, it could reflect the proposed supramodal spatial attention mechanism (Foxe and Snyder, 2011). However, given that α -band suppression occurs in relation to both somatotopic and external tactile location, it has also been related to tactile remapping, that is, the transformation of tactile-spatial information from somatotopic to external coding. Results of previous studies that investigated the spatial coding of tactually induced α -band modulation have been consistent with the role of α -band activity as a supramodal spatial attentional mechanism. In contrast, a specific mechanism of how α -band activity may mediate remapping has not been put forward, and previous findings have not conclusively established whether, or how, α -band modulation mediates the remapping process itself (Buchholz et al., 2011; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019).

Even at a descriptive level, two main issues have precluded disentangling these two possible roles of α -band activity. First, the spatial location of tactile stimulation has usually been task relevant in previous experiments (Buchholz et al., 2011, 2013; Bauer et al., 2012; Ruzzoli and Soto-Faraco, 2014; Schubert et al., 2019). Therefore, α -band lateralization in those studies may have been due exclusively to attentional (re-)orienting and prioritization. Notably, external-spatial effects of touch on behavior have been observed even when a tactile stimulus is task irrelevant (Azañón et al., 2010; Ossandón et al., 2015), supporting the view that tactile remapping occurs automatically (Badde et al., 2014). Thus, if α -band activity truly mediates tactile remapping, it should accompany the processing of task-irrelevant tactile stimuli, with or without observable behavioral results.

Second, if α -band modulation played a causal role in tactile remapping, it should precede any externally oriented behavior in response to a touch. Yet, whereas estimates for the time requirements of tactile remapping range from 20 to 300 ms (Yamamoto and Kitazawa, 2001; Azañón and Soto-Faraco, 2008; Overvliet et al., 2011; Brandes and Heed, 2015) α -band modulation has been demonstrated to develop gradually in tasks that implement long delays of >1 s between attentional cue and tactile stimulus or between tactile stimulus and a subsequent response (Buchholz et al., 2011, 2013; van Ede et al., 2011, 2014; Bauer et al., 2012; Schubert et al., 2015). This time course may imply that α -band

modulation reflects processes that result from, rather than mediate, tactile-spatial transformation.

To scrutinize the role of α -band activity in tactile remapping and tactually induced attention, participants performed an overt visual search task in which the external location of a tactile cue was either informative (task relevant) or uninformative (task irrelevant) about target location. To evaluate overlapping tactile, visual, and oculomotor electroencephalogram (EEG) activity, we employed a massive univariate deconvolution analysis approach (Ehinger and Dimigen, 2019) that separates brain responses to multiple types of events that occur at variable intervals between each other. This approach allowed us to let participants behave freely and without requiring artificial delays.

Materials and Methods

Participants

Thirty-six participants took part in the study after giving written consent. We excluded three of them from the analysis because they did not complete the experiment and two because data were corrupted. We thus report on 31 participants (28 females; mean age: 25 years; range: 18–44; SD = 6.8). All experimental procedures were approved by the ethics committee of the German Psychological Society (TH 122014).

Visual stimuli

Figure 1A,B illustrates a visual search trial. The search stimulus was presented on a 23" monitor (Samsung Syncmaster P23701), on a gray background that extended 42.2° horizontally and 23.7° vertically. It consisted of a grid of six by eight white symbols located within the screen central 30° × 18° (~36 × 21.6 cm on screen), with a single circle target located among 47 circle distractors for which a short, vertical line intersected the lower pole. This type of stimulus is known to require serial searching, as inferred from profiles of reaction time (Treisman and Souther, 1985; Zelinsky and Sheinberg, 1997). Stimuli were generated and presented with Psychtoolbox 3 (Brainard, 1997; Kleiner et al., 2007), executed on MATLAB R2007b (The MathWorks).

Tactile stimulation

Tactile stimuli were 25 ms long, suprathreshold, 200-Hz vibrations, delivered to the back of the participant's hand in the middle of the dorsum (aligned with the middle finger). Stimulation was produced by electromagnetic solenoid-type tactors (Dancer Design) that were attached to the skin with medical tape. Tactors were driven linearly by the voltage generated via a Mini Piezo-Tactile Controller/Amplifier (Dancer Design). To mask any noise that could originate from the stimulators, participants wore earplugs and white noise was played from a central loudspeaker located below the screen.

Experimental design and data acquisition

Procedure

Figure 1A illustrates the sequence of a single trial. Participants sat at a viewing distance of 66 cm from the monitor, resting their hands comfortably on the table in front of them, that is, on a horizontal plane between the participant and the vertical plane of the screen, with one hand below each side of the screen. The hands were positioned so that the stimulators were 30 cm apart, roughly aligned with the outer column of the search grid. Vision of the hands was not prevented. Across blocks, hand position was altered between uncrossed and crossed postures, so that the right hand rested either under the right (uncrossed) or left side (crossed) of the screen, and vice versa for the left hand. When the hands were crossed, the forearms touched each other. Tactile cues occurred at the beginning of every trial, between 150 and 250 ms (uniform random distribution) after the appearance of the search display. The location of the target was randomly assigned on each trial, and therefore it could be located either on the left or right side of the screen. The experiment was divided in two parts. In one part, the tactile cue was informative; participants were instructed that the search target was located on the side of the search display under which the stimulated hand was located. In

Figure 1. Experimental procedure and deconvolution analysis approach. **A**, Progression of a single trial. **B**, Example of visual search. Stimuli consisted of a grid of six by eight symbols with a single circle target (here in fourth row, eighth column) located among 47 distractors. Searches started at the center. Blue and red traces show eye-tracking data (each dot represents a sample acquired at 500 Hz) of one informative and one uninformative trial. In these two examples, the tactile stimulation was provided to the hand located below the right side of the screen. **C**, Experimental conditions follow a 2 (left/right) $\times$ 2 (crossed/uncrossed) $\times$ 2 (informative/uninformative) fully factorial design. The star is used throughout the article as abbreviation for tactile stimulation. Informative and uninformative conditions were conducted as separate parts of the experiment. All other factors varied on a trial-by-trial basis. **D**, Schematic of the deconvolution model. The relationship between the continuous α power $\alpha_{power(t)}$ of each EEG channel per participant and the independent predictors, specified in the design matrix $X_{(t,\tau)}$, is estimated by finding corresponding regressors beta values β that minimize the model error $\epsilon(t)$. To disentangle overlapping effects, $X_{(t,\tau)}$ is expanded in time, so each experimental predictor is replicated at each sampling point τ between -500 and 800 ms around its respective event (i.e., at 250 Hz, each experimental predictor is implemented as 325 model predictors, each at a different sampling point along the time interval). Our illustration shows only a subset of the predictors and sampling points. In the example shown here, a tactile stimulus occurs on crossed hands at time t ; this stimulus is followed by two saccades at 292 and 500 ms, respectively. Accordingly, the design matrix codes the intercept and the hand crossing predictor as value 1 and -1 at sampling points $\tau = 0$, and as value 0 at all other sampling points. For the eye movement events, the intercept predictor at time t is coded as value 1 at sampling points $\tau = -500$ and $\tau = -292$, and 0 at the sampling points preceding or following each respective saccade.

informative trials the tactile cue was 100% valid. This instruction was formulated externally, in that it pertained to the hands' location in space, and not to the stimulated hand body side. In the second part, the tactile cue was uninformative; participants were instructed that tactile stimulation was unrelated to the search task. This tactile cue was, therefore, only 50% valid. The order of the uninformative and informative experiment parts was balanced across participants.

Trials started with the appearance of the search display after the experimenter had confirmed that participants fixated a central fixation dot. The trial ended after the participant had fixated the target, operationalized as the detection of a fixation within a cell of size $3.74^\circ \times 3.05^\circ$ centered on the target, for >500 ms. Trials were aborted if no such target fixation occurred within 12 s.

Figure 1C illustrates the experimental conditions. Participants performed 48 blocks with 24 trials each. We, thus, collected 144 trials per combination of our three experimental factors hand crossing, task relevance, and anatomical side of touch. Before testing, participants received a practice block of 16 trials without tactile stimulation.

Eye tracking

Eye movements were recorded with a video-based infrared Eyelink 1000 system (SR Research Ltd.), using the monocular remote tracking mode at 500-Hz sampling rate. Eye movements were defined using the systems' default parameters, and the system standard 13-point calibration procedure was performed to achieve an average calibration error $<0.5^\circ$ and a maximal calibration error $<1.0^\circ$.

EEG acquisition

Electrophysiological data were recorded using Ag/AgCl electrodes with a BrainAmp DC amplifier (Brain Products GmbH) with a sampling rate of 1000 Hz. A total of 73 electrodes was placed according to the 10–10 system (Acharya et al., 2016), with location AFz serving as ground and the right earlobe as reference. Three electro-oculogram channels were placed in a triangular montage, with channels on the forehead and on the left and right infraorbital rim (Plöchl et al., 2012). The impedances of all electrodes were below 5 k Ω .

EEG preprocessing

Data were preprocessed and analyzed with MATLAB R2015a using custom scripts and the third-party toolboxes EEGLAB (Delorme and Makeig, 2004), Fieldtrip (Oostenveld et al., 2011), and Unfold (Ehinger and Dimigen, 2019).

The complete continuous EEG data were evaluated for the presence of artifactual segments and bad channels with an automatic, custom procedure based on amplitude, high-frequency noise, and linear-trend thresholds (detailed description and analysis scripts are available at <https://osf.io/d7xc6>). Channels or segments identified as artifactual were removed in subsequent analyses. We removed channels entirely when >15% of experimental data would have had to be discarded because of artifacts. This procedure excluded, on average, 0.77 channels per subject (0/1/2/3/4 channels removed in 16/9/4/1/1 participants, respectively). Excluded channels were replaced by interpolated channels based on spherical interpolation as implemented in EEGLAB's *pop_interp* function. Next, we identified ocular and muscular artifactual components by independent component analysis and removed these components from the raw data. We identified eye-movement related components via an automatic algorithm based on the variance ratio between fixation and saccade periods (Plöchl et al., 2012). We defined muscle-related components as components in which total power above 20 Hz was larger than power below 20 Hz. We removed, on average, 24.2 (SD = 7.3) independent components per subject.

Data analysis

Behavior

We evaluated the overall effect of cueing on reaction times with a three-way repeated-measures ANOVA, with factors anatomical side of touch (left/right), hand crossing (uncrossed/crossed), and task relevance (informative/uninformative). Individual main and interaction effects, consecutive two-way ANOVAs, and *post hoc* comparison were evaluated with a significance threshold of 0.05, Bonferroni-adjusted for all possible multiple comparisons per-test.

We evaluated the effect of task relevance on the probability to make a saccade that ended on the cued side of the search display separately for uncrossed and crossed hand trials, using logistic models. We counted saccades in 50-ms bins from the moment of stimulation until 600 ms after, resulting in 12 time bins and, accordingly, 12 separate models. The logistic models were defined as a multilevel model with a task relevance predictor and an individual intercept per subject: $\text{logit}(P(y_{(i)} = \text{cued sided})) = \beta_0 + X_{\text{Task Relevance}(i)}\beta + \alpha_{j(i)} + \text{error}_{(i)}$, where i indexes the current trial and $j(i)$ the corresponding participant. y is the dependent variable indicating whether or not a saccade ended on the cued side in each trial. β_0 is the model average intercept and β is the effect of task relevance. $X_{\text{Task Relevance}}$ represents a vector that indicates whether the trial was informative or uninformative. Finally, α represents the participant-wise intercepts. We report results as the probabilities associated with each condition $1/(1 + \exp(-(\beta_0 + \beta)))$ tested against the probability of no effect ($p = 0.5$) at a significance threshold Bonferroni-adjusted for multiple comparisons (12 time bins $\times$ 2 levels of task relevance = 24 tests).

Deconvolution models

EEG time series represent the summed changes measured on a given electrode at every sampling point, caused by all sensory, cognitive, and motor events that took place around the time of the recording. Thus, the effects of multiple events are usually intermingled within the EEG signal. In the present study, the EEG activity in response to tactile stimulation is potentially overshadowed by EEG activity related to visual stimulation and eye movements. To separate these different signals, we combined massive-univariate linear deconvolution modeling (Smith and Kutas, 2015a) with generalized additive modeling (Ehinger and Dimigen, 2019). In massive univariate EEG modeling, regression of scalp electrical activity on the experimental factors of the study is performed independently for each sample and electrode. This approach has gained track over the last decade as a way to analyze EEG data obtained from complex setups that combine multiple experimental factors (Groppe et al., 2011; Pernet et al., 2011; Smith and Kutas, 2015b). Linear deconvolution is maybe best known from functional magnetic resonance imaging analysis

(Dale, 1999), but it has been applied successfully in EEG and MEG both for time-series (Lütkenhöner, 2010; Dandekar et al., 2012; Kristensen et al., 2017; Cornelissen et al., 2019) and time-frequency (Litvak et al., 2013) analysis. Disentangling different types of events, such as stimuli and motor responses, is possible in this framework because events occur with varying temporal overlap during the course of an experiment, so that an event's effect over time overlaps with other events' effects of different time points with each occurrence, allowing separation of effects with standard regression methods. In other words, deconvolution determines time-extended effects of discrete experimental events that occur with varying temporal overlap during the experiment. In our study, saccades and the appearance of the search display are discrete events, but their respective effects on EEG signals potentially extend for several hundreds of milliseconds and, thus, overlap in time. Deconvolution allows dissociating these overlapping signals (Smith and Kutas, 2015b; Ehinger and Dimigen, 2019). Generalized additive modeling allows accounting for nonlinear effects in linear regression analysis (Wood, 2017), and has been implemented in the Unfold toolbox for EEG deconvolution through spline functions. We used this approach to account for saccadic movement amplitudes in the horizontal and vertical dimension. Finally, regression results can be analyzed across participants in a second-level analysis by spatiotemporal clustering of significant regression β values. This method renders data-driven statistical evaluation without the need to specify spatial or temporal regions of interest (ROIs; detailed below in section Second-level analysis).

The present analysis focused on α -band activity, because this frequency range has been consistently associated with the processing of tactile information, both for anatomic and external spatial coding. First, we down-sampled EEG signals to 250 Hz. Then, the continuous EEG dataset was bandpass-filtered with a sync zero-phase FIR filter (369 samples Hamming windowed filter, 6-dB cutoff at 7.8 and 16.1 Hz, 2.25 transition bandwidth) and Hilbert-transformed. We computed the signal's instantaneous power from the Hilbert transform output. Although the temporal resolution of this processed signal is determined by the previous band pass step, sharp modulations of α -band activity in the range observed here (~ 1 dB) are smeared only for ~ 1 oscillatory cycle in practice. Signal power at each sampling point was normalized in dB to its ratio with the respective channel mean power during a baseline period ranging from -450 to 0 ms before each trial's start, that is, at least 150 ms before tactile stimulation.

We fitted each individual participant's normalized instantaneous α power with a deconvolution model. The model accounted for effects of tactile stimulation, search display appearance, and saccade initiation, by using the following set of predictors:

- for the tactile stimulation event, we entered main effects of factors hand crossing and task relevance, as well as their interaction
- for the search display appearance event, we entered an intercept relative to the time of search display appearance.
- for the activity related to ocular movement events, we entered an intercept and 10 spline predictors for the continuous variables of horizontal and vertical movement components, relative to the start of the saccade. We used splines instead of simple linear regressors because the effects of some saccade parameters, such as movement amplitude, on visual event-related potentials have been shown to be markedly non-linear (Dandekar et al., 2012; Kaunitz et al., 2014; Ehinger and Dimigen, 2019). Movement was computed as the position difference between saccade end and start, separately for the horizontal and vertical dimension. Because each eye movement instance contributes to the regression, effects observed for the ocular movement predictors are comparable to a trial-by-trial analysis with respect to saccadic latency and, thus, account for latency variability.

Massive univariate deconvolution regressed the continuous estimate of α power on this set of predictors. Figure 1D gives a brief overview of how deconvolution is implemented in the regression model [see also the excellent and highly accessible introduction to deconvolution analysis in Ehinger and Dimigen (2019) and implementation considerations in Smith and Kutas (2015b)]. For the different types of events in our experiment, the formula of the deconvolution model in a given channel across

time t is given by: $\alpha_{power(t)} = X_{(t,\tau)}\beta + \text{error}_{(t)}$, with α_{power} denoting the continuous estimate of α power. The deconvolution matrix $X_{(t,\tau)}$ is constructed by column concatenation of individual matrices for each event type (Fig. 1D):

$$X_{(t,\tau)} = [X_{tactile_stim(t,\tau)} X_{display_appearance(t,\tau)} X_{saccade(t,\tau)}].$$

Each event type matrix consists, in turn, in a concatenation of “time-expanded” matrices (see below), one for each of the event type predictors described above. For instance, for the tactile stimulation event, the corresponding matrix has the form:

$$X_{tactile_stim(t,\tau)} = [X_{intercept(t,\tau)} X_{hand_crossing(t,\tau)} X_{task_relevance(t,\tau)} X_{hand_crossing \times task_relevance(t,\tau)}].$$

These time-expanded matrices are generated by assigning a predictor to every time-lag τ in the time interval of interest around the occurrence of the respective event. In the present study, we defined the time interval of interest around each event as the time from 500 ms before to 800 ms after the event. Figure 1D illustrates time expansion with the example of a tactile stimulus that occurred at time t . The time-expanded matrix for the intercept of the hand stimulation predictor $X_{intercept(t,\tau)}$ adds the predictor value 1 at positions: $(t - 500, \tau = -500), \dots, (t, \tau = 0), \dots, (t + 800, \tau = 800)$ (Fig. 1D, leftmost matrix). In this way, predictors are assigned not only to each event but to every time-lag around the event. Solving the deconvolution model for β was accomplished by using LSMR, an iterative algorithm for sparse least-square problems (Fong and Saunders, 2011). The deconvolution model was run separately for each channel and participant. Finally, all event-predictor estimates were then entered in a second level analysis, as described below.

We devised two different deconvolution models to analyze different aspects of α -band modulation in our experiment. The first analysis focused on the topography of α -band modulation relative to stimulus location, and we refer to it as the “topography analysis” from here on. For this analysis, we re-coded channel topography relative to the anatomic site of stimulation. We flipped EEG channels for trials in which the left hand had been stimulated with respect to the left and right scalp side (Buchholz et al., 2011; Schubert et al., 2015). Additionally, we reversed the sign of the horizontal eye movement component for left-hand trials to account for flipping their EEG topography. This procedure effectively codes EEG signals as if all stimuli had occurred on the right hand, allowing us to pool trials across anatomical side of touch to increase statistical power.

The second analysis focused on hemispheric differences of α -band activity, and we refer to it as the “hemispheric difference analysis” from here on. We used the difference in power between homologous channels over the two hemispheres as dependent variable. This strategy reduced the number of channels to 33 (76 channels minus 10 midline electrodes, divided by 2). Furthermore, we did not pool left and right stimulus locations as in the topography analysis. Rather, keeping left and right stimulation separate allowed deriving contralateral and ipsilateral effects by comparing right minus left stimulation. Accordingly, we applied a deconvolution model that was equivalent to that of our first analysis but included a predictor of anatomic stimulation side and the respective interactions.

Second-level analysis

We assessed the statistical significance of α -band modulation associated with the predictors of our deconvolution models with a second-level group analysis. To this end, participants' β values of each model predictor were tested against zero at each event time-lag and channel with t tests. We applied a cluster-based permutation test (Maris and Oostenveld, 2007) to control the elevated family-wise error-rate because of testing multiple channels and sampling points. We clustered all samples that resulted in a t value with an associated $p < 0.05$ based on proximity on the scalp or in time, and the sum of the corresponding t values was calculated for each of the resulting clusters. We

compared empirical cluster values with the distribution of a 2000-samples permutation that we constructed by taking the maximal cluster value of each permutation iteration. Permutation iterations were obtained by randomly flipping, subject-by-subject, the sign of a given predictor across all channels and time samples (Good, 2000). This is based on the rationale that, if the estimated effects were not consistently different from zero, changing the sign of their values would result in similar clusters than the one obtained from the actual estimate. In contrast, if a factor results in a consistent effect, randomly changing predictor signs (across participants) would remove its effect. For any given predictor, we considered the determined empirical clusters significant at a $p < 0.05$ if their summed t value was smaller than 2.5th percentile, or higher than the 97.5th percentile of the permutation distribution. To further control for testing multiple predictors (Ehinger et al., 2015), we applied a Bonferroni correction, dividing the obtained p values by the number of predictors of the model (contra-ipsi models: six predictors, $\alpha = 0.008$; difference models: eight predictors, $\alpha = 0.005$; connectivity comparisons: six predictors, $\alpha = 0.008$).

Hypotheses

We used the results of the modeling analyses to evaluate the following hypotheses testing the involvement of α -band power modulation in tactile remapping.

First, α -band activity should be modulated in external-spatial coordinates by tactile stimulation in both informative and uninformative trials if the proposal that automatic tactile remapping is reflected in α -band activity is correct. Notably, the neural signature of an automatic process should be evident even if no behavioral effect is evident. In terms of our topography analysis model, α -band modulation should be evident in a significant hand crossing effect, without a significant interaction with task relevance; moreover, there should be an effect of hand crossing specifically in uninformative trials. In terms of our hemispheric difference analysis α -band lateralization should be evident in a significant two-way interaction of hand crossing and anatomical side of touch but, critically, without an interaction with task relevance.

Second, the externally coded modulation should be observed following tactile stimulation but preceding the subsequent externally guided eye-movement behavior. This could manifest as a significant crossing effect after tactile stimulation that occurs before any significant behavioral modulation. Alternatively, a modulation of α activity may precede eye movement events. This modulation could take the form of a significant cluster in the time course of the model's ocular movement intercept if effects are generally related to eye movements, independent of saccade endpoints in space. If effects depend on saccade endpoints, these effects would be evident in the spline predictors.

Connectivity analysis

We hypothesized that information is transferred differently between primary somatosensory and posterior parietal regions depending on hand posture. To investigate information transfer, we analyzed connectivity measures between channels located above the respective brain regions that were also modulated by our task. Modulation of the respective channels by anatomic and external spatial codes has been previously reported (Buchholz et al., 2011; Schubert et al., 2015), and those studies demonstrated the related brain sources to include primary somatosensory and posterior parietal regions. We calculated the imaginary part of complex coherency in α -band activity as a way to measure oscillatory coupling that is not explained by spurious volume conduction (Nolte et al., 2004). Connectivity measures like coherency and imaginary coherency must be computed across trials and, therefore, cannot be calculated as a continuous measure that could be included in a deconvolution model. Therefore, we performed connectivity analysis by comparing estimates of condition averages and, thus, we could not directly control for the effect of eye movements. However, the spectral signature of eye movements artefactual component comprises frequencies below and above α and are not expected to confound our α -band analysis and are effectively removed by ICA (Plöchl et al., 2012).

For the connectivity analysis, we first re-coded EEG channels, as described above for the first time-frequency analysis, by flipping the EEG topography of left-hand trials, so as to pool right-hand and left-hand stimulation. Next, we defined ROIs from central and posterior channels that had shown the strongest and longest modulation by anatomic or external spatial coding in the deconvolution analysis (central contralateral: “C3”; central ipsilateral: “C4”; posterior contralateral: “P5-P7-PO7”; posterior ipsilateral: “P6-P8-PO8”). We then applied a sliding Fourier transform over the data of each trial, using a single Hanning taper with variable temporal window size consisting of three cycles at 9–15 Hz and 15-ms step size. Next, we calculated the imaginary part of coherency between each combination of channel pairs across ROIs, separately for each factor level combination of hand crossing and task relevance. Finally, we determined a single value per ROI pair as the average across all possible between-ROI channel pairings.

Open data and code accessibility

The code and model results used to produce the figures below are available at <https://osf.io/d7xc6>. The original EEG and eye-tracking datasets are available on request.

Results

Participants performed an overt visual search task in which they had to find a target among 47 distractors (Fig. 1). At the beginning of each trial, one hand received a brief vibrotactile stimulus. This stimulus was either task relevant, informing about the side of the search display on which the target was located, or it was uninformative and, thus, task irrelevant. The hands were placed underneath the search display in an uncrossed or a crossed posture, allowing to determine whether modulation of behavior and electrophysiological α -band responses were coded anatomically, that is, based on which hand was stimulated, or externally, that is, based on the side of space on which the stimulated hand was placed.

Performance

Figure 2A illustrates participants' overall task performance and reaction time distribution. Performance was almost at ceiling, with the search target being acquired in 98.3% of trials within the 12-s time limit. Across participants, the average search time was 2511 ms (SD = 500). Figure 2B illustrates the effect of tactile stimulation on search time. A repeated-measures ANOVA with factors anatomical side of touch (left vs right hand), hand crossing (uncrossed vs crossed) and task relevance (informative vs uninformative), revealed a significant main effect of task relevance ($F_{(30,1)} = 132.3$, $p < 0.001$) and a significant three-way interaction ($F_{(30,1)} = 8.8$, $p = 0.006$). *Post hoc* comparison showed that search was 1156 ms faster with informative than uninformative cues ($t_{(30)} = -11.5$, $p < 0.001$, Cohen's effect size $d_z = 2.06$), a reduction of search time by 37%.

We followed up on the three-way interaction with separate two-way ANOVAs for informative and uninformative cues. For informative tactile stimulation, there was a significant main effect of hand crossing ($F_{(30,1)} = 10.7$, $p = 0.002$) and an interaction of hand crossing and anatomical side of touch ($F_{(30,1)} = 14.3$, $p < 0.001$). *Post hoc* comparison indicated that hand crossing slowed search by 126 ms (uncrossed: 1856 ms; crossed: 1983 ms, $t_{(30)} = -3.2$, $p = 0.002$, $d_z = 0.58$). Furthermore, the effect of anatomical side of touch depended on hand crossing: with uncrossed hands, search time was 84 ms faster after right as compared with left hand stimulation, though this difference was not significant after Bonferroni correction ($t_{(30)} = 2.22$, $p = 0.03$, $d_z = 0.4$; corrected α significance level: 0.008). In contrast, with crossed hands, search time was significantly faster by 126 ms

Figure 2. *A*, Search performance. Thin gray lines show the search time distribution per participant; the black line reflects the group-average distribution. Gray circles on top indicate each participant's mean search time; the red line indicates the average across participants. Gray circles on the right indicate the proportion of misses per participant. *B*, Search time split by task relevance. Participants' individual means are shown as gray circles. Error bars are condition mean $\pm$ SEM; LU: left hand stimulation uncrossed posture; RU: right uncrossed; LC: left crossed; RC: right crossed. *C*, Probability to fixate the cued side in uncrossed-hands trials, binned into 50-ms segments following tactile stimulation. Blue and red lines indicate fixation probability for informative and uninformative trials, respectively. Shaded area reflects SEM. Asterisks demarks probability different from 0.5 at a multiple-comparison Bonferroni-adjusted α for 24 tests (two conditions $\times$ 12 bins of 50-ms width, ranging from 0 to 600 ms; see Materials and Methods). *D*, As *C* but for crossed-hands trials. Fixation side is coded relative to the stimulated hand's location in space. Accordingly, the complement of the depicted probability corresponds to the probability of fixating on the side of the search display that corresponded with the anatomic body side of tactile stimulation.

after left as compared with right hand stimulation ($t_{(30)} = 2.8$, $p = 0.008$; $d_z = 0.5$). This reversed hand effect suggests the observed processing advantage depended on the external location of touch in space, with tactile stimulation on the right side of space being more effective than those on the left. In sum, touch was an effective spatial cue, and hand crossing resulted in a small but significant cost.

Exploration patterns after tactile stimulation are biased only when stimulation is task relevant

The effect of tactile stimulation on total search time was paralleled by modulation of visual exploration behavior. Figure 3A,B illustrates fixation positions of all participants for all experimental conditions. Fixations were centered on the search elements. In uninformative trials, exploration was distributed uniformly across items. In contrast, in informative trials, eye movements were directed almost exclusively to the side of the screen indicated by the tactile cue in external coordinates. The only exceptions were a few saccades that were initiated before tactile stimulation.

This overall exploration pattern emerged directly following tactile stimulation. Figure 3C,D shows the probability to fixate and the latency distributions of the first three saccades after stimulation for informative and uninformative trials, grouped according to the hemifield in which the saccade ended. Saccade probability decreased from the moment of stimulation until around 100 ms after stimulation, to then increase again (Fig. 3C,D, darkest traces); this pattern is typical for saccades following

Figure 3. Exploration patterns and latency to move after stimulation. **A, B**, Spatial fixation distribution of fixations for uninformative (**A**) and informative (**B**) cues, separately for each combination of anatomical side of stimulation and hand (columns 1–4). Panels display random subsamples of 50% of all participants' pooled data to retain visibility of individual fixations. **C, D**, Fixation probability and latency of the first three saccades according to the side of the screen on which they end, for uninformative (**C**) and informative (**D**) cues, separately for each combination of anatomical side of stimulation and hand. Bars in the upper section of each panel show the probability to fixate left or right for the first (dark), second (middle), and third (light) saccade after tactile stimulation. Dotted traces in the lower part of each panel illustrate the probability of saccades to end left or right over time, binned in 50-ms intervals, relative to the time of stimulation. Continuous lines with shaded area reflect the mean difference ($\pm$ SEM) between left and right relative frequencies.

sensory stimulation and has been associated with saccadic inhibition because of stimulation (Ossandón et al., 2015). After this inhibitory phase, first saccades were biased to the left in uninformative trials, as it is usually the case during exploratory free viewing (Ossandón et al., 2014, 2015). Second and third saccades following stimulation were balanced across hemifields. In informative trials, second and third saccades ended on the side of the display that had been cued by the tactile stimulus. The preference for saccades to the cued side of the search display (Fig. 3C,D, continuous lines) became apparent after $\sim$ 100 ms with uncrossed hands, but not until $\sim$ 200 ms with crossed hands.

We statistically tested the modulation of saccade end-points by tactile stimulation with mixed-effect logistic models for the averaged fixation probability of every 50-ms bin from the moment of tactile stimulation until 600 ms after stimulation, separately for uncrossed and crossed hand trials. For informative trials with uncrossed hands (Fig. 2C), the first time bin in which fixation probability to the tactually cued side differed statistically from chance was the 100- to 150-ms time bin. Fixation probability increased to above 95% in the following time bins, statistically

confirming the above reported observations. In contrast, exploration was unbiased by the cue in uninformative trials, with the exception of the interval between 450 and 550 ms, in which fixation probability was slightly but significantly biased toward the side indicated by the uninformative cue.

For crossed hands (Fig. 2D), saccade probability toward the tactually cued side refers to instances in which tactile location had been transformed from anatomic to external location. For informative trials, the first time bin in which saccades were more probable toward the tactually cued side of the search display was the 200- to 250-ms time bin. Fixation probability increased to above 90% in the following time bins. Exploration was unaffected by the cue in uninformative trials. At no time did we observe a bias toward the anatomic side of stimulation in crossed hand trials. This finding suggests that saccades were guided by the external location of tactile cues.

Anatomically and externally coded α -band EEG responses to tactile stimulation

Analysis up to this point demonstrated that tactile stimulation affected visual search behavior, and that this modulation

Figure 4. Absolute and relative spectra of all channels in all conditions. **A**, Absolute power spectra of each subject (thin lines) and averages (thick lines) for the baseline period between -500 and 0 ms prior tactile stimulation (green) and for the period between 0 and $+500$ ms after stimulation (orange). This baseline period includes a period between 250 and 350 ms before trial start, given that the tactile stimulus occurred between 150 and 250 ms after stimulus appearance. **B**, Time-frequency chart aligned to the moment of tactile stimulation in dB with respect to a baseline period between -600 and -400 ms before tactile stimulation (window size: 500 ms; padding: 1000 ms; single hanning taper; moving step: 15 ms).

depended on the relevance of tactile stimulation for the search task. Next, we focus on the modulation of α -band activity by touch and saccades in the context of visual exploration. In general, our task manipulations resulted in modulation of oscillatory activity that was specific for the α -band range around 10 Hz (Fig. 4A), evident both during baseline and after stimulation (Fig. 4B).

We statistically evaluated the effect of tactile stimulation on α -band activity, restricted to 9 – 15 Hz, with a massive-univariate deconvolution modeling approach that used predictors for tactile stimulation, the start of the search display, and saccade programming on EEG instantaneous (normalized) power. The deconvolution model isolates effects of tactile stimulation in the context of visual processing and unrestricted saccades across extended periods of time. As a critical feature, we modeled horizontal and vertical saccade displacement with a set of splines to remove any confounding effects of the systematic behavioral saccade direction biases that we had identified in search behavior.

We performed two analyses on α -band activity, one focusing on the topography of α -band modulation across the scalp, and the other focusing on hemispheric differences of α -band activity. The topography analysis recoded all data channels as if all tactile stimuli had been applied to the right hand (see Materials and Methods). Cluster-based permutation testing identified significant clusters of power modulation for the predictors associated with the tactile stimulation model intercept, the main effects of hand crossing and task relevance, and of their interaction. Figure 5A–D display the α -band modulation associated with each of these predictors as topographic maps. A deconvolution model regresses the dependent variable (α -band activity) on the predictors at each sampling point in an interval around the predictor event (e.g., tactile stimulation, search display appearance); therefore, the topographic maps illustrate the effect of the experimental factors across time around each type of event at each electrode, ultimately showing how the effect of our experimental manipulations unfolds in the α -band signal over time and space. Maps display the average β weight of each subsequent 75 -ms interval in the time range from 150 ms before to 750 ms after the event.

The intercept was negative surrounding the time of stimulation in most channels both ipsilaterally and contralaterally (significant cluster from -228 to $+800$ ms, $p < 0.0005$; Fig. 5A), indicating that tactile stimulation was accompanied by a general α -band power decrease. The fact that this decrease began before tactile stimulation was probably related to the predictability of

tactile stimulation to occur in temporal vicinity of the trial's start, even if it was jittered. We observed a similar, global suppression effect for the factor task relevance that was stronger in informative than uninformative trials, but offset by ~ 400 ms (cluster from $+392$ to $+800$ ms, $p < 0.0005$; Fig. 5B). Hand crossing was associated with α -band suppression in a lateralized cluster ipsilateral to the stimulated hand (cluster from $+156$ to $+796$ ms, $p = 0.0025$; Fig. 5C); that is, when the hands were crossed, α -band suppression was contralateral to the external location of the tactile stimulus. Accordingly, this effect cannot be explained by tactile stimulus processing in the primary somatosensory areas corresponding to the stimulated hand. Finally, the interaction between the two factors was accompanied by another cluster ipsilateral to the stimulated hand (cluster from $+324$ to $+800$ ms, $p = 0.005$; Fig. 5D), indicating that the hand crossing effect was larger for informative than uninformative trials. A specific contrast looking for a hand crossing effect only in uninformative trials did not reveal a significant cluster. The effect of hand crossing and its interaction with task relevance can be more easily appreciated in Figure 6A, which shows the sum of the involved effects for each factor combination (excluding the model intercept for clarity), as well as the difference between uncrossed and crossed postures, separately for informative and uninformative trials. In informative trials, α -band activity was suppressed contralateral to the external side of stimulation, mostly at posterior sensors. Such modulation was not observable for uninformative trials.

Multiple studies have suggested that differences of α -band power between the two hemispheres is indicative of attentional lateralization (Foxe and Snyder, 2011). Therefore, we performed a second analysis to directly assess the imbalance of α -band activity between the two hemispheres by analyzing the difference of homologous channels of the left minus the right hemisphere (for instance, C3 minus C4), again with deconvolution modeling. In this analysis, we did not collapse across left-hand and right-hand stimulation, to allow assessing effects of contralateral and ipsilateral stimulation as left minus right stimulation trials (see Materials and Methods). Accordingly, the model comprised the same predictors for hand crossing and task relevance as the topography analysis, but in addition included predictors for the main effect of anatomical side of touch as well as the interactions with this factor. There were no significant clusters for the model Intercept and the hand crossing factor, both of which could have revealed a hemispheric laterality/dominance effect independent of anatomic or external location. Figure 5E–G illustrates the topographies for predictors that were significantly modulated by tactile stimulation. The main effect of anatomical side of touch (Fig. 5E) was evident as stronger α suppression for a circumscribed cluster of central channels contralateral to the stimulated hand (cluster from $+64$ to $+800$ ms, $p < 0.0005$). Given that the dependent measure of the analysis was the difference of left minus right channels, this suppression effect indicates stronger suppression anatomically contralateral to tactile stimulation. There were no significant clusters for the interaction of anatomical side of touch and task relevance, suggesting that anatomic coding was not modulated by task relevance. The interaction of anatomical side of touch and hand crossing (Fig. 5F) and the three-way interaction of anatomical side of touch, hand crossing, and task relevance (Fig. 5G), revealed significant clusters of α suppression when corrected per predictor (side $\times$ crossing: $+276$ to $+596$ ms, $p = 0.049$, three-way interaction: $+324$ to $+600$ ms, $p = 0.019$). However, these clusters did not survive correction for multiple model factors. However, we note that they

Figure 5. Modulation of α -band (9–15 Hz) power by tactile stimulation during visual search. **A–D**, Average EEG topographies of the power assigned to relevant predictors of the deconvolution model in which all stimuli were coded as if they had occurred on the right hand. From top to bottom, Rows show the tactile stimulation intercept (**A**), main effects of task relevance (**B**) and hand crossing (**C**), and their interaction (**D**). **E–G**, Modulation of lateralized α -band power by tactile stimulation during visual search. α -Band activity was subtracted between homologous channels (left minus right hemisphere). Topographies show the left hemisphere, from which right hemisphere activity was subtracted. Midline electrodes are omitted. From top to bottom, Rows show the effect of anatomical hand stimulated (**E**), the interaction of anatomical side of stimulation and hand crossing (**F**), and the three-way interaction of anatomical side of stimulation, hand crossing, and task relevance (**G**). In all panels, each topoplots depicts the average of a 75-ms time interval. Time 0 is the moment of tactile stimulation. Dots indicate sensors that have been assigned to a significant spatiotemporal cluster by cluster-based permutation testing in at least one sampling point covered by the topoplots. Gray dots indicate $p < 0.05$ corrected for the multiple electrode and time samples tested per factor; black dots indicate significance after correcting for the number of permutation tests per model (see Materials and Methods).

were spatially congruent with the clusters revealed by our first analysis and show, during informative trials, a reversal of α modulation between central and posterior channels in the contrast between uncrossed and crossed postures (Fig. 6B,C, top row). This difference between central and posterior channels indicates that the respective signals must reflect distinct phenomena. Given the direction of the modulations, the central process is based on somatotopic coding, and the posterior process is based in external coding. Finally, Figure 6D–G illustrates the relationship, during informative trials, between α -band modulation and saccade latency after tactile stimulation, with the data split according to three saccade latency quantiles. The somatotopic modulation at central electrodes occurs early and, at least for the second and third quantile, before the saccades. In contrast, the external modulation at posterior electrodes, in the crossed hands condition, occurs after the saccades for all quantiles.

In summary, the results of both the topography analysis and the hemispheric difference analysis revealed suppression of

α -band activity following tactile stimulation. These suppression effects were independent of hand posture at contralateral central channels, indicating that α -band modulation was affected by anatomic coding. In contrast, α -band activity was modulated by hand posture at anatomically ipsilateral central and posterior channels, suggesting that touch affected neural activity in an external spatial code. This latter effect was evident only in informative trials, that is, when the stimulus location was task relevant.

α -Band EEG responses to the search display and saccades are discernible from responses to touch

The deconvolution model also accounted for visual and saccade effects, aiming to isolate them from effects of tactile stimulation. Figure 7A,B illustrates that α -band activity was suppressed by the appearance of the search display. Statistically significant clusters were present only in the topography analysis (Fig. 7A), in which α -band activity was tested over the two hemispheres. α -Band power was globally suppressed from -256 to $+648$

Figure 6. *A*, Topography analysis α -band suppression for the different experimental conditions and respective contrasts. The topoplots display the sum of the different effects associated with tactile stimulation (excluding the model intercept for clarity), in the interval between +300 and +750 ms after stimulation, that is, the time interval in which the hand crossing and task relevance interaction was significant. *B*, *C*, Hemispheric difference analysis for left (*B*) and right (*C*) hand stimulation, showing the modulation of differences in α -band between left and right hemisphere electrodes for the same interval. Here, red color indicates that α power is higher in the left compared with the right hemisphere, and blue colors vice versa. *D–G*, Progression of α suppression for informative trials according to the hemispheric difference analysis, at central (*D*, *E*) and posterior (*F*, *G*) electrodes for uncrossed (*D*, *F*) and crossed (*E*, *G*) postures. The thin, colored lines reflect α -band modulation for three equal divisions of the data according to the latency of the first saccade after stimulation. The dotted black lines reflect α -band modulation for all trials. Colored areas show the distribution of saccade latencies for the three depicted quantiles, and the associated dotted vertical lines the corresponding median value.

($p < 0.0005$) first globally and then more locally to posterior and right-side electrodes, and enhanced again from +416 to +796 ms (end of the analysis window, $p < 0.0005$). In the hemisphere difference analysis (Fig. 7*B*), clusters obtained with permutation tests did not survive correction for multiple testing. Once the search display was presented, participants were allowed to saccade without restriction, resulting in the production of a sequence of fixations and saccades (see behavioral results above). Therefore, to disentangle the effects of tactile stimulation from the ones related to saccade programming and subsequent visual processing, we included all saccadic events that started within 800 ms of trial start. Figure 7*C,D* shows the saccade event intercept for both contra-ipsilateral (Fig. 7*C*) and interhemispheric difference (Fig. 7*D*) analyses. Only the topography analysis revealed significant clusters of α -band activity modulation, with a global cluster of inhibition from +132 to +796 ms (end of the analysis window, $p < 0.0005$). These results imply that each new saccade event further suppressed α -band activity above and beyond any suppression because of the appearance of the search display as well as tactile stimulation. It is noteworthy that we did not find any α -band

modulation before saccade initiation. This observation suggests that α -band activity does not reflect saccade programming, neither as a global signal nor as a lateralized, hemispheric difference signal. This lack of α -band modulation before saccades is in stark contrast with a modulation of α -band activity that depended on both the horizontal and vertical distance of the performed saccade (Fig. 7*E,F*). With each saccade, α -band activity was not just modulated globally (Fig. 7*C*), but it was also suppressed in the hemisphere contralateral to saccade direction (Fig. 7*F*), with stronger suppression the larger the saccade. This graded effect was long-lasting, but was strongest ~50–200 ms after the saccade (Fig. 7*F*). Notably, as for the other saccade predictors, no modulation of α -band activity was evident before saccade initiation. This suggests that the graded effect of saccade amplitude was a result of saccade execution, and not related to the planning of the saccade.

EEG connectivity suggests that external coding is mediated by ipsilateral somatosensory cortex

Next, we asked how information is routed from somatosensory regions to posterior parietal cortex. Given the prominent effects

Figure 7. α -Band (9–15 Hz) modulation by the occurrence of the search display and saccades. **A, B**, Effect of display appearance for the first analysis (**A**) and the second analysis (**B**). **C, D**, As **A** but for the saccade event intercept. **E, F**, Effects of differently sized vectors of horizontal (top panels) and vertical (bottom panels) saccadic displacement obtained from spline predictors in the deconvolution modeling for the topography (**E**) and hemisphere difference (**F**) analyses. Traces show activity of the summed spline predictors, averaged over those posterior channels that were significantly modulated.

in the α range, we hypothesized that externally coded α -band modulation may be mediated by oscillatory coupling with somatosensory cortex. More specifically, we conjectured that the somatosensory cortex contralateral to tactile stimulation, in which tactile information first arrives in cortex, would exhibit coupling with the posterior regions contralateral to the tactile stimulation's external location. Accordingly, with uncrossed hands, coupling should be intra-hemispherical, between somatosensory and posterior parieto-occipital cortex of the same hemisphere. In contrast, with crossed hands, anatomic and external location belong to opposite hemifields, and therefore coupling should be evident cross-hemispherically, between the somatosensory cortex contralateral, and the posterior parieto-occipital cortex ipsilateral, to the anatomic side of tactile stimulation. Notably, connectivity and signal power reflect independent neuronal mechanisms. Therefore, it is possible that, even if α -band power was suppressed following tactile stimulation, α -band connectivity may nevertheless be present or enhanced. If so, this connectivity pattern would suggest a role of this frequency band for tactile-spatial transformations through connectivity rather than local power modulation.

We tested connectivity between the specific central and parietal channels of the two hemispheres in which we had observed anatomically and externally coded spatial modulation of α -band activity, as evident in α -band modulation in response to our experimental factors of hand crossing and task relevance. We assessed connectivity as the imaginary part of the complex coherence. Before tactile stimulation, connectivity between central and parieto-occipital channels was enhanced intra-hemispherically (Fig. 8B,E), but not cross-hemispherically (Fig. 8C,D), independent of hand posture and task relevance of tactile stimulation. Cross-hemispheric coupling was, however, evident after tactile stimulation. However, contrary to our hypothesis, we did not observe cross-hemispheric coupling between central and posterior channels (Fig. 8C,D). Instead, cross-hemispheric coupling was evident between the two parieto-occipital regions, but only during informative trials (difference cluster from +400 to +800 ms, $p < 0.001$; Fig. 8F). This cross-hemispheric coupling was accompanied by intra-hemispheric coupling of the ipsilateral somatosensory and parieto-occipital channels (Fig. 8E). Although ipsilateral coupling was present in informative and uninformative trials, a modulation of connectivity by hand posture was apparent only in informative trials.

Figure 8. α -Range coupling between central and parietal regions, assessed as the imaginary part of coherency cross-hemispherically (**A,C,E,F**) and intra-hemispherically (**B,D**). Top and bottom plots, Results for informative and uninformative trials, respectively. Different columns illustrate the coupling between each pair of ROIs. Dark and light lines indicate uncrossed and crossed hand data, respectively. Black line shows the difference between postures, with a red line denoting a significant temporal cluster. Shaded areas represent SEM.

Together, these results are incompatible with direct transfer of information by α -band coupling between somatosensory and posterior parieto-occipital areas across hemispheres as a means of transforming anatomically coded into externally coded tactile information to guide attention. Instead, they suggest that inter-hemispheric transfer of tactile information is mediated in a first step by coupling between somatosensory areas, later followed by intrahemispheric coupling between somatosensory and posterior parieto-occipital areas.

Discussion

The present study aimed at characterizing the role of α -band modulation during the processing of tactile-spatial information. In particular, we asked whether the occurrence and timing of α -band modulation supports the notion that this brain signal may be a mediator of tactile-spatial transformations. By employing a massive univariate deconvolution modeling approach, we disentangled the overlapping signals related to different events, namely visual stimulation, tactile stimulation, and the preparation and execution of eye movements.

Our study revealed three main results. First, touch affected saccade behavior exclusively in an external reference frame, and only when it was task relevant. This effect on behavior was evident within 100 ms for uncrossed hands, and within 200 ms for crossed hands. Second, α -band suppression was modulated somatotopically in contralateral somatosensory cortex, but externally in ipsilateral somatosensory and posterior parietal cortex. External-spatial effects of touch on α activity and interhemispheric connectivity between somatosensory and posterior parietal regions were evident only when touch provided task-relevant information. Third, saccadic behavior was modulated by touch before a change of α -band suppression was evident in the EEG signal. Together, these findings are inconsistent with the notion that α -band activity directly reflects tactile-spatial transformation and suggest that the involvement of this oscillatory signal, instead, reflects supramodal, attention-related consequences of remapped tactile information.

Behavioral correlates of tactile stimulation

Tactile spatial information guided overt visual search when it was informative. This effect was fast and consistent: after 100 ms, saccades were biased toward the external side of touch; subsequent saccades remained almost exclusively on the cued side.

When the hands were crossed, this effect was slowed by 100 ms, but nonetheless directed externally. While a purely external effect of touch on saccades is in agreement with previous studies (Groh and Sparks, 1996; Blanke and Grüsser, 2001; Overvliet et al., 2011; Buchholz et al., 2012), both saccades and reaches toward tactile locations can exhibit trajectories that initially deviate toward the anatomic side of the tactile event (Groh and Sparks, 1996; Overvliet et al., 2011; Brandes and Heed, 2015). In those previous experiments, the tactile stimulus location was the movement goal. Thus, the tactile stimulus was within the frame of spatial attention required by those tasks. The occurrence of attentional capture has been reported to depend on whether the stimulus is located within the spatial frame defined by the task (Belopolsky et al., 2007; Theeuwes, 2010). In the present experiment, in contrast, stimulus location only served as a global cue within the search task's spatial frame (i.e., the monitor), but was itself located outside that space. This arrangement avoided attentional capture, which would have drawn saccades directly to the hand stimulus and have interfered with the search task: instead, saccades were affected within the visual search task space.

Our present results corroborate those obtained in our previous study (Ossandón et al., 2015), suggesting that spatial biases elicited by tactile stimulation are expressed solely in an external reference frame when a tactile stimulus is not the movement goal. In our previous study, free image exploration was biased toward the external-spatial side of a task-irrelevant tactile cue. In contrast, here, in the context of a search task, participants ignored uninformative tactile cues entirely. This finding indicates that the use of tactile spatial information during free viewing is not mandatory but can be strategically discounted.

Previous estimates of when external tactile information is first available have been inconsistent, ranging from 20 to 360 ms (Yamamoto and Kitazawa, 2001; Azañón and Soto-Faraco, 2008; Overvliet et al., 2011; Brandes and Heed, 2015). At 100-ms response time, externally directed saccade responses were considerably faster here, and conflict resulting from crossed limbs was resolved after 200 ms, consistent with our previous report about hand reach corrections to tactile stimuli (Brandes and Heed, 2015). The time from programming a saccade to its execution has been estimated to lie around 100 ms (Hanes and Carpenter, 1999; Reingold and Stampe, 1999). Likewise, we and others have reported tactile saccadic inhibition effects within 100 ms from stimulation (Akerfelt et al., 2006; Ossandón et al.,

2015). Before 100-ms postcue, saccades are directed randomly to all locations on the screen; afterward, saccade direction integrates tactile stimulus location. The fact that saccades followed touch to uncrossed hands in our study principally supports the suggestion that transformation of somatotopic into external touch location is almost immediate (Brandes and Heed, 2015). This notion was based on comparing the time taken to initiate a turn toward visual and tactile stimuli during a hand reach. Tactually evoked turns were only 20 ms slower after tactile stimulation to uncrossed limbs than to visual stimuli at identical locations, thus suggesting a very short estimate for the computation of an external-spatial location of touch. However, one must bear in mind that the present study's time estimates are averages across many trials, and that the stimulation only affected some saccades at 100 ms, becoming more consistent only at later time points.

Lateralized α -band suppression in response to tactile stimulation

Previous work has consistently shown that spatial cueing of tactile stimulation is followed by central and posterior parietal α -band suppression in the interval between the cue and presentation of the tactile stimulus (Jones et al., 2010; Haegens et al., 2011; van Ede et al., 2011; Bauer et al., 2012). Comparison of hand postures revealed that these α -band suppression effects depend on the cued hand over central electrodes, but that they additionally reflect the cued space at posterior parietal electrodes (Schubert et al., 2015).

Other studies have, instead, investigated α -band modulation after (as opposed to before) the presentation of a tactile stimulus. In one study, participants received tactile stimulation on the index or little finger of one hand while fixating the same hand's middle finger (Buchholz et al., 2011). While planning a saccade to the tactile location, posterior parietal α -band activity was suppressed in the hemisphere opposite to finger location relative to gaze, as it has been reported for visual paradigms as well (Gutteling et al., 2015). In another study, touch to uncrossed and crossed hands also resulted in externally coded parietal α -band suppression (Schubert et al., 2019). Several studies have reported separable anatomic and external modulation of α -activity related to tactile stimulation. Previous EEG and MEG studies reported circumscribed α -band modulation at central sensors and source-localized this activity to primary somatosensory areas (Jones et al., 2010; Haegens et al., 2011; van Ede et al., 2011; Schubert et al., 2015). In contrast, modulation at parieto-occipital sensors is usually more wide-spread and has been source-localized to the posterior parietal lobe, the intraparietal sulcus, and occipital areas (Buchholz et al., 2011, 2013; Schubert et al., 2015, 2019).

Here, a tactile cue was used to modulate attentional and motor processing of an ongoing task that involved frequent saccades. α -Band suppression was similarly lateralized as in tasks that require attention in preparation for tactile stimulation. Crucially, parieto-occipital lateralization in external coordinates occurred only when touch was informative. Given the absence of a behavioral bias during uninformative trials, the presence of posterior α lateralization in an external reference frame when the touch was uninformative would have been suggestive of a role of α activity in tactile remapping proper. Its absence, in contrast, suggests that the lateralization observed in informative trials is related to subsequent spatial processing.

By design, hand crossing experiments involve a conflict between somatotopic and external reference frames in the crossed posture. Therefore, one alternative interpretation of the

crossing effects observed here is that they reflect effects of stimulus-response incompatibility, given that anatomic information of the tactile stimulus is incompatible with the related saccadic response. Stimulus-response compatibility effects have, however, been related to increases in fronto-central theta activity (Cohen and Donner, 2013; Wang et al., 2014), so that it appears unlikely that the lateralized suppression of α shown here is related to the resolution of stimulus-response conflicts.

Viewed together, externally coded, parietal α -band modulation occurs in a wide range of contexts, both during visual and tactile processing, prior and after stimulation. Rather than indexing, or even mediating, tactile-spatial transformation processes, it seems to reflect subsequent spatial processing. Our experiment cannot reveal which particular processes were mediated by α -band modulation, but likely candidate processes may be the further elaboration of tactile-spatial features, an attentional modulation of visual processing (either of the cued hemifield or the actual visual target), and a more general, supramodal, spatial prioritization process.

Tactile stimulation affected not only the power of α -band activity, but also its inter-regional coupling. We had hypothesized that information may be routed directly from somatosensory cortex of one hemisphere to the parietal cortex of the other when the hands are crossed. Such direct coupling could have been interpreted as a means of remapping somatotopic into external information through *ad hoc* connectivity of the relevant parts of two differently coded spatial maps. Contrary to this hypothesis, during crossed-hand informative trials, connectivity first manifested inter-hemispherically between central electrodes, and then intra-hemispherically, contralateral to the external stimulus location. This unexpected result might nevertheless be consistent with studies that have shown that unilateral tactile stimuli are processed not only in the somatotopically contralateral, but also in the ipsilateral primary somatosensory cortex already at early stages of processing (Sutherland and Tang, 2006; Tamè et al., 2012, 2015, 2019). The early oscillatory coupling observed in our present study might be related to this interaction between primary somatosensory areas. If so, then our results suggest that this interaction between primary cortices is likely instrumental for subsequent processing in the hemisphere ipsilateral to the stimulated anatomic side during the processing of externally coded tactile-spatial information.

Behavior modulation precedes α -band modulation

In the present study, we observed a sharp modulation of α power related to the tactile events, evident already 64 ms after stimulation for central α -suppression associated with somatosensory processing, indicating that changes in α activity can be detected at short latency with our analysis methods. Critically, however, spatially specific posterior α -lateralization occurred only after 150–300 ms and, thus, disassociated from the fast oculomotor search responses, especially when considering that saccade programming is presumably complete 100 ms before the overt saccade. If α -band lateralization were causal for saccade direction, it should precede, rather than follow, saccades. We explicitly modeled changes in α -band activity in relation to the subsequent saccadic behavior and did not observe modulation before saccade execution, speaking against it being directly linked to the observed oculomotor behavior. Finally, modulatory effects of α -band connectivity first occurred >400 ms following tactile stimulation, which, just like the observed power modulation, was later in time than the externally directed behavior. The consistent divergence of α -related modulation and externally oriented behavior suggests

that the spatial processes mediated by posterior α -band lateralization are unlikely to be related directly to tactile remapping and to exogenously oriented, low-latency eye movement responses.

References

- Acharya JN, Hani AJ, Cheek J, Thirumala P, Tsuchida TN (2016) American clinical neurophysiology society guideline 2: guidelines for standard electrode position nomenclature. *Neurodiagn J* 56:245–252.
- Akerfelt A, Colonius H, Diederich A (2006) Visual-tactile saccadic inhibition. *Exp Brain Res* 169:554–563.
- Azañón E, Soto-Faraco S (2008) Changing reference frames during the encoding of tactile events. *Curr Biol* 18:1044–1049.
- Azañón E, Camacho K, Soto-Faraco S (2010) Tactile remapping beyond space. *Eur J Neurosci* 31:1858–1867.
- Badde S, Heed T, Röder B (2014) Processing load impairs coordinate integration for the localization of touch. *Atten Percept Psychophys* 76:1136–1150.
- Bauer M, Kennett S, Driver J (2012) Attentional selection of location and modality in vision and touch modulates low-frequency activity in associated sensory cortices. *J Neurophysiol* 107:2342–2351.
- Belopolsky AV, Zwaan L, Theeuwes J, Kramer AF (2007) The size of an attentional window modulates attentional capture by color singletons. *Psychon Bull Rev* 14:934–938.
- Blanke O, Grüsser OJ (2001) Saccades guided by somatosensory stimuli. *Vision Res* 41:2407–2412.
- Brainard DH (1997) The psychophysics toolbox. *Spat Vis* 10:433–436.
- Brandes J, Heed T (2015) Reach trajectories characterize tactile localization for sensorimotor decision making. *J Neurosci* 35:13648–13658.
- Buchholz VN, Jensen O, Medendorp WP (2011) Multiple reference frames in cortical oscillatory activity during tactile remapping for saccades. *J Neurosci* 31:16864–16871.
- Buchholz VN, Goonetilleke SC, Medendorp WP, Corneil BD (2012) Greater benefits of multisensory integration during complex sensorimotor transformations. *J Neurophysiol* 107:3135–3143.
- Buchholz VN, Jensen O, Medendorp WP (2013) Parietal oscillations code nonvisual reach targets relative to gaze and body. *J Neurosci* 33:3492–3499.
- Cohen MX, Donner TH (2013) Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *J Neurophysiol* 110:2752–2763.
- Cornelissen T, Sassenhagen J, Vö ML-H (2019) Improving free-viewing fixation-related EEG potentials with continuous-time regression. *J Neurosci Methods* 313:77–94.
- Dale AM (1999) Optimal experimental design for event-related fMRI. *Hum Brain Mapp* 8:109–114.
- Dandekar S, Privitera C, Carney T, Klein SA (2012) Neural saccadic response estimation during natural viewing. *J Neurophysiol* 107:1776–1790.
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134:9–21.
- Ehinger BV, Dimigen O (2019) Unfold: an integrated toolbox for overlap correction, non-linear modeling, and regression-based EEG analysis. *PeerJ* 7:e7838.
- Ehinger BV, König P, Ossandón JP (2015) Predictions of visual content across eye movements and their modulation by inferred information. *J Neurosci* 35:7403–7413.
- Fong DC, Saunders M (2011) LSMR: an iterative algorithm for sparse least-squares problems. *SIAM J Sci Comput* 33:2950–2971.
- Foxe JJ, Snyder AC (2011) The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front Psychol* 2:154.
- Good PI (2000) Permutation tests: a practical guide to resampling methods for testing hypotheses. Ed 2. New York: Springer.
- Groß JM, Sparks DL (1996) Saccades to somatosensory targets. I. behavioral characteristics. *J Neurophysiol* 75:412–427.
- Groppe DM, Urbach TP, Kutas M (2011) Mass univariate analysis of event-related brain potentials/fields I: a critical tutorial review. *Psychophysiology* 48:1711–1725.
- Gutteling TP, Selen LPJ, Medendorp WP (2015) Parallax-sensitive remapping of visual space in occipito-parietal alpha-band activity during whole-body motion. *J Neurophysiol* 113:1574–1584.
- Haegens S, Händel BF, Jensen O (2011) Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *J Neurosci* 31:5197–5204.
- Hanes DP, Carpenter RH (1999) Countermanding saccades in humans. *Vision Res* 39:2777–2791.
- Jensen O, Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 4:186.
- Jones SR, Kerr CE, Wan Q, Pritchett DL, Ha M, Moore CI (2010) Modulation of the mu rhythm in primary somatosensory cortex. *J Neurosci* 30:13760–13765.
- Kaunitz LN, Kamienskowski JE, Varatharajah A, Sigman M, Quian R, Ison MJ (2014) Looking for a face in the crowd: fixation-related potentials in an eye-movement visual search task. *Neuroimage* 89:297–305.
- Kleiner M, Brainard D, Pelli D (2007) What's new in Psychtoolbox-3? *Percept* 36, ECVF Abstract Supplement: 14.
- Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53:63–88.
- Kristensen E, Rivet B, Guérin-Dugué A (2017) Estimation of overlapped eye fixation related potentials: the general linear model, a more flexible framework than the ADJAR algorithm. *J Eye Mov Res* 10:1–27.
- Litvak V, Jha A, Flandin G, Friston K (2013) Convolution models for induced electromagnetic responses. *Neuroimage* 64:388–398.
- Lütkenhöner B (2010) Baseline correction of overlapping event-related responses using a linear deconvolution technique. *Neuroimage* 52:86–96.
- Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods* 164:177–190.
- Nolte G, Bai O, Wheaton L, Mari Z, Vorbach S, Hallett M (2004) Identifying true brain interaction from EEG data using the imaginary part of coherency. *Clin Neurophysiol* 115:2292–2307.
- Oostenveld R, Fries P, Maris E, Schoffelen JM (2011) FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci* 2011:156869.
- Ossandón JP, Onat S, König P (2014) Spatial biases in viewing behavior. *J Vis* 14:20–20.
- Ossandón JP, König P, Heed T (2015) Irrelevant tactile stimulation biases visual exploration in external coordinates. *Sci Rep* 5:10664.
- Overvliet KE, Azañón E, Soto-Faraco S (2011) Somatosensory saccades reveal the timing of tactile spatial remapping. *Neuropsychologia* 49:3046–3052.
- Pernet CR, Chauveau N, Gaspar C, Rousselet GA (2011) LIMO EEG: a toolbox for hierarchical linear modeling of electroencephalographic data. *Comput Intell Neurosci* 2011:831409.
- Plöchl M, Ossandón JP, König P (2012) Combining EEG and eye tracking: identification, characterization, and correction of eye movement artifacts in electroencephalographic data. *Front Hum Neurosci* 6:278.
- Reingold EM, Stampe DM (1999) Saccadic inhibition in complex visual tasks. In: *Current oculomotor research: physiological and psychological aspects* (Becker W, Deubel H, Mergner T, eds), pp 249–255. Boston: Springer US.
- Ruzzoli M, Soto-Faraco S (2014) Alpha stimulation of the human parietal cortex attunes tactile perception to external space. *Curr Biol* 24:329–332.
- Schubert JTW, Buchholz VN, Föcker J, Engel AK, Röder B, Heed T (2015) Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *Neuroimage* 117:417–428.
- Schubert JTW, Buchholz VN, Föcker J, Engel AK, Röder B, Heed T (2019) Alpha-band oscillations reflect external spatial coding for tactile stimuli in sighted, but not in congenitally blind humans. *Sci Rep* 9:9215.
- Schürmann M, Başar E (2001) Functional aspects of alpha oscillations in the EEG. *Int J Psychophysiol* 39:151–158.
- Smith NJ, Kutas M (2015a) Regression-based estimation of ERP waveforms: I. The rERP framework. *Psychophysiology* 52:157–168.
- Smith NJ, Kutas M (2015b) Regression-based estimation of ERP waveforms: II. Nonlinear effects, overlap correction, and practical considerations. *Psychophysiology* 52:169–181.
- Sutherland MT, Tang AC (2006) Reliable detection of bilateral activation in human primary somatosensory cortex by unilateral median nerve stimulation. *Neuroimage* 33:1042–1054.
- Tamè L, Braun C, Lingnau A, Schwarzbach J, Demarchi G, Li Hegner Y, Farnè A, Pavani F (2012) The contribution of primary and secondary

- somatosensory cortices to the representation of body parts and body sides: an fMRI adaptation study. *J Cogn Neurosci* 24:2306–2320.
- Tamè L, Pavani F, Papadelis C, Farnè A, Braun C (2015) Early integration of bilateral touch in the primary somatosensory cortex. *Hum Brain Mapp* 36:1506–1523.
- Tamè L, Azañón E, Longo MR (2019) A conceptual model of tactile processing across body features of size, shape, side, and spatial location. *Front Psychol* 10:291.
- Theeuwes J (2010) Top-down and bottom-up control of visual selection. *Acta Psychol (Amst)* 135:77–99.
- Treisman A, Souther J (1985) Search Asymmetry: a diagnostic for preattentive processing of separable features. *J Exp Psychol Gen* 114:285–310.
- van Ede F, de Lange F, Jensen O, Maris E (2011) Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *J Neurosci* 31:2016–2024.
- van Ede F, Szebényi S, Maris E (2014) Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *Neuroimage* 97:134–141.
- Wang K, Li Q, Zheng Y, Wang H, Liu X (2014) Temporal and spectral profiles of stimulus–stimulus and stimulus–response conflict processing. *Neuroimage* 89:280–288.
- Wood SN (2017) Generalized additive models: an introduction with R. Boca Raton: CRC Press.
- Yamamoto S, Kitazawa S (2001) Reversal of subjective temporal order due to arm crossing. *Nat Neurosci* 4:759–765.
- Zelinsky G, Sheinberg D (1997) Eye movements during parallel–serial visual search. *J Exp Psychol Hum Percept Perform* 23:244–262.