



## Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention



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### ABSTRACT

Touch can be localized either on the skin in anatomical coordinates, or, after integration with posture, in external space. Sighted individuals are thought to encode touch in both coordinate systems concurrently, whereas congenitally blind individuals exhibit a strong bias for using anatomical coordinates. We investigated the neural correlates of this differential dominance in the use of anatomical and external reference frames by assessing oscillatory brain activity during a tactile spatial attention task. The EEG was recorded while sighted and congenitally blind adults received tactile stimulation to uncrossed and crossed hands while detecting rare tactile targets at one cued hand only.

In the sighted group, oscillatory alpha-band activity (8–12 Hz) in the cue–target interval was reduced contralaterally and enhanced ipsilaterally with uncrossed hands. Hand crossing attenuated the degree of posterior parietal alpha-band lateralization, indicating that attention deployment was affected by external spatial coordinates. Beamforming suggested that this posture effect originated in the posterior parietal cortex. In contrast, cue-related lateralization of central alpha-band as well as of beta-band activity (16–24 Hz) were unaffected by hand crossing, suggesting that these oscillations exclusively encode anatomical coordinates. In the blind group, central alpha-band activity was lateralized, but did not change across postures. The pattern of beta-band activity was indistinguishable between groups. Because the neural mechanisms for posterior alpha-band generation seem to be linked to developmental vision, we speculate that the lack of this neural mechanism in blind individuals is related to their preferred use of anatomical over external spatial codes in sensory processing.

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### Introduction

The location of a touch is defined by at least two types of reference frames: Touch is localized with respect to the skin, as is evident in the homuncular organization of primary somatosensory cortex. In addition, to localize touch in external space, skin location must be combined with current body posture. Thus, whereas the right hand will always be on the right side in anatomical terms, it can occupy the left side of external space when it is crossed over the midline. When attention has to be directed to a hand, the brain could use an anatomical or an external code to represent the location at which a touch is expected. In fact, the brain appears to use both of these codes concurrently (Eimer et al., 2003; Heed and Röder, 2010). This dual coding becomes evident in contexts in which anatomical and external coordinates are incongruent, as is the case with crossed hands. In this situation, behavioral

performance in tactile localization tasks is regularly impaired, evident in increased localization errors and prolonged reaction time (Shore et al., 2002; Yamamoto and Kitazawa, 2001; for a review see Heed and Azañón, 2014). Similarly, markers of spatial attention in event-related potentials (ERP) are reduced when touch is applied to crossed as compared to uncrossed hands (Eimer et al., 2003), presumably indexing the coordinate conflict.

Tactile attentional deployment is reflected not only in ERP, but also in oscillatory brain activity as measured with EEG and MEG. The power of oscillatory activity in the alpha and beta frequency range has been found to be reduced in the hemisphere contralateral to the side to which tactile attention is directed (Bauer et al., 2012; Haegens et al., 2012; Van Ede et al., 2011). However, it is not yet clear which reference frames guide such lateralization of oscillatory brain activity, because experiments investigating oscillatory activity during tactile attentional orienting have not varied hand posture. However, when eye and hand movements are planned towards tactile target stimuli, posterior alpha-band oscillations during the movement planning phase were reported to reflect external coordinates, whereas central alpha- and

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central and posterior beta-band activity appear to be modulated only by anatomical coordinates and to be unaffected by external spatial coordinates (Buchholz et al., 2011, 2013).

The transformation from anatomical into external coordinates seems to critically depend on the availability of visual input after birth. In contrast to the sighted, congenitally blind individuals were not affected by hand crossing in a tactile localization task (Röder et al., 2004). Similarly, ERP markers for tactile attention were not modulated by posture in this group (Röder et al., 2008). These findings suggest that congenitally blind individuals rely on anatomical rather than on external coordinates for tactile localization. However, the neural changes that result in the abandonment of an external reference frame after congenital blindness are not yet understood.

Thus, the goal of the present study was twofold. First, we aimed at characterizing which types of reference frames are reflected in alpha- and beta-band oscillatory activity during the orienting of tactile spatial attention. Second, we sought to investigate the role of the visual system in defining the neural mechanisms that mediate these reference frames. To these ends, we analyzed oscillatory activity in the EEG signal of sighted and congenitally blind participants who oriented their attention towards one hand in expectation of a tactile stimulus, while holding their hands in uncrossed and crossed postures.

## Materials and methods

We examined data for which results of tactile ERPs have been previously reported (Röder et al., 2008). We confine our description of experimental methods to those essential for the present analyses.

### Participants

The dataset comprised 12 congenitally blind individuals (mean age: 26.2 years, range 20–35 years, 6 female, 7 right handed, 5 ambidextrous) and 12 sighted individuals matched in age and handedness (mean age: 23.5 years; range: 19–34 years; five female, all right handed). All participants were blindfolded during the experiment. All blind participants were blind from birth due to peripheral defects and were either totally blind or did not have more than diffuse light perception. The experiment was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (2013) and the ethical requirements of the University of Marburg, where the data for this study were acquired.

### Stimuli and procedure

Tactile stimuli were either frequent standard stimuli ( $p = 0.75$ ), or rare ( $p = 0.25$ ) deviant stimuli presented with an equal probability in a random sequence to the left and the right hand. They were presented 1000 ms after an auditory cue that instructed participants to attend one of their hands. Participants had to respond as fast and accurately as possible to rare tactile deviants presented to the cued hand (“targets”,  $p = 0.125$ ), and to ignore standard stimuli at the attended hand, as well as all stimuli presented to the other hand. The auditory cue was a centrally presented, low- or high-pitched auditory cue (900 and 1000 Hz, respectively) referring to a hand independent of hand posture (rather than to a side of space), to avoid any emphasis on external coordinates. The paradigm follows the idea of Hillyard and colleagues and allows investigating effects of attentional orienting both before and during stimulus processing by keeping physical stimulation the same across conditions (Hillyard et al., 1973).

Tactile stimulation consisted of two metallic pins (diameter: 0.8 mm) that were briefly raised by 0.35 mm. For standard stimuli, the pins were raised, and lowered again after 200 ms. For deviant stimuli, the pins were raised twice for 95 ms, with a 10 ms pause in-between, again resulting in a total duration of 200 ms. Participants had to respond when the stimulus was a rare tactile deviant stimulus at the attended

hand, and to ignore all other stimuli (Fig. 1). The next trial started after a random interval of 1200–1600 ms following the onset of the tactile stimulus. Hands were placed 40 cm apart on a table in front of the participant, positioned either in an uncrossed or in a crossed posture (alternated blockwise, order counterbalanced across participants). Detection responses were given with a foot pedal that was placed underneath the left foot in half of the experiment, and under the right in the other half. The experiment consisted of 16 blocks with 96 standards and 32 deviants in each block. Each of the eight original conditions (two hand postures, two attention cues, two stimulus locations) before aggregating comprised 192 standard stimuli. The analysis included only trials in which standard stimuli were presented and in which, accordingly, no response was required.

### EEG recording

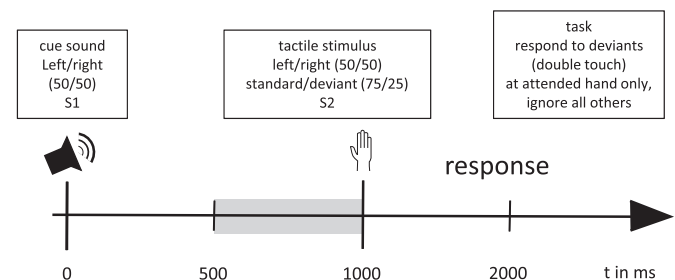
Continuous EEG data was recorded from 61 equidistantly arranged scalp electrodes. The sampling rate was 500 Hz with an analog passband filter of 0.1–100 Hz of the amplifiers (Synamps, Neuroscan). To monitor eye movements, additional electrodes were placed near the outer canthi of the eyes and under the right eye. Electrode impedances were kept below 5 k $\Omega$ . The right earlobe served as reference during recording.

### Analysis of behavioral performance

We calculated the sensitivity measure  $d'$  for each participant and each hand posture. The  $d'$  measure combines correct responses to targets (“hits”) and incorrect responses (“false alarms”) (Green and Swets, 1966). The  $d'$  scores were analyzed with an ANOVA for repeated measures with the between factor Group and the within factor Posture (cf. Röder et al., 2008).

### Analysis of EEG data

Event-related potentials were reported elsewhere (Röder et al., 2008). Here we analyzed EEG oscillatory activity. Analysis of the EEG data was performed using FieldTrip (Oostenveld et al., 2011) in the Matlab environment (Mathworks, Natick, MA). Data was re-referenced to an average reference (Schneider et al., 2008). Line noise was removed by subtracting 50 and 100 Hz components estimated by discrete Fourier transform (van Ede et al., 2011). Trials were segmented into 2.5 s epochs lasting from 0.5 s before auditory cue onset (that is, 1.5 s before tactile stimulus onset) until 1.0 s post-stimulus. We analyzed only trials that contained standard stimuli and were, thus, free of response-related processing. Trials in which participants had erroneously responded (false alarms), as well as trials that contained late responses from the previous trial, were excluded.



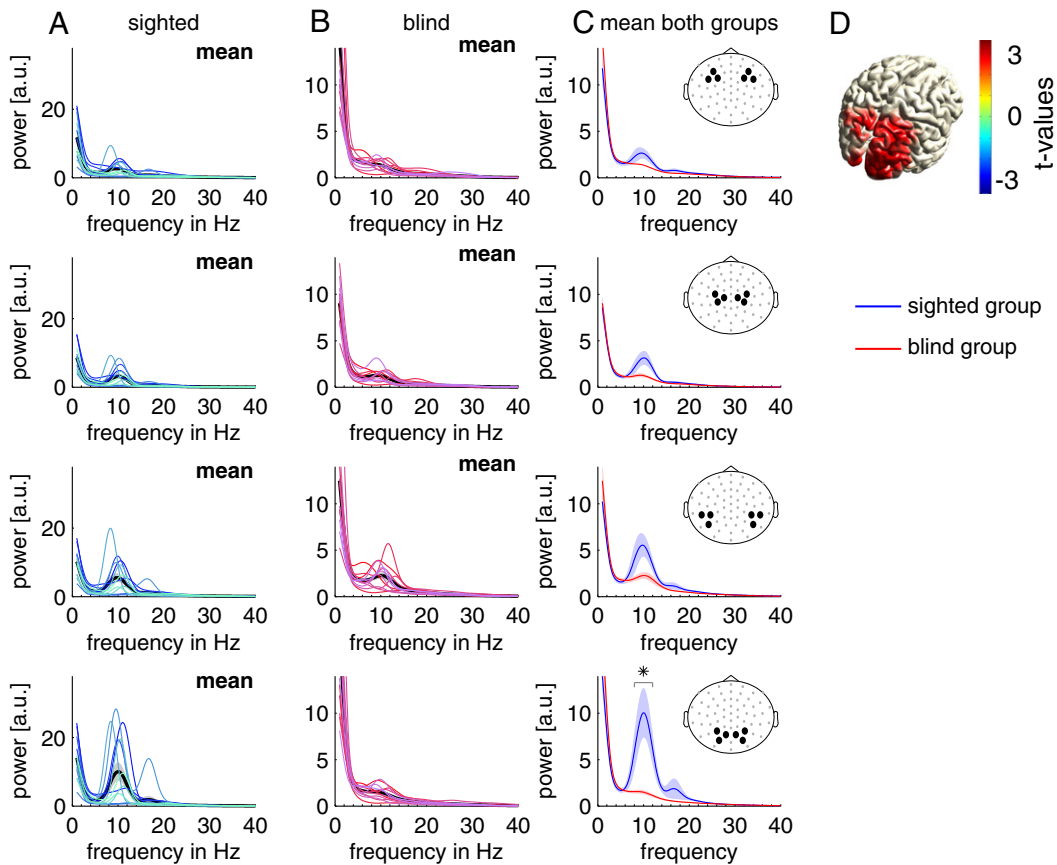
**Fig. 1.** Schematic trial structure. Each trial started with an auditory cue to indicate the task relevant finger during that trial ( $t = 0$ ). After 1000 ms a tactile stimulus (standards and deviants) was presented either to the left or to the right hand. Participants had to respond to rare tactile deviants at the attended hand only while ignoring all other stimuli (see text for details). Posture of the hands (uncrossed vs. crossed) was alternated blockwise. We report oscillatory activity during the time between cue and stimulus (marked by gray shaded box).

The full length of each epoch including baseline and cue–target interval was visually inspected. Trials were removed if they were contaminated by muscle or eye artifacts. For sensor level analysis, data were pooled over left and right hands by remapping electrode channels to ipsi- and contralateral recording sites relative to the attended hand (regardless of its position in space). Consequently, data are presented here as if attention had always been directed to a the right hand, and the left (right) hemisphere denotes the contralateral (ipsilateral) hemisphere (see Fig. S1 for topographies of unpooled and not yet remapped data). Frequency analysis was performed for frequencies of 2–40 Hz, computed based on the Fourier approach using a Hanning taper of 500 ms that was moved along the time axis in steps of 20 ms. Time–frequency representations of single trials were averaged for each participant and condition. We defined four clusters of interest (see Figs. 4 & 6): a frontal cluster (electrode positions approximately corresponding to F3/4, FC1/2, and FC3/4 of the 10–10 system (Oostenveld and Praamstra, 2001)), a central cluster (approximately C1/2, C3/4, and CP1/2), a parietal cluster (approximately CP3/4, P3/4, and CP5/6), and a parieto-occipital cluster (approximately PO1/2, O1/2, and P3/4). Even though the signal recorded by an EEG electrode cannot be directly attributed to the underlying cortical region, we were particularly interested in the activity of the central and parietal clusters for three reasons: first, tactile stimulation at the hand has been reported to evoke alpha-band desynchronization in the EEG signal over contralateral electrode sites such as C3/4 (Nierula et al., 2013). Second, oscillatory activity in the alpha and beta frequency range over central and parieto-occipital sensors has been related to the orienting

of tactile attention (Haegens et al., 2012; van Ede et al., 2011). Third, different oscillatory activity at posterior and central sensors has been associated with the use of different spatial reference frames during movement planning towards tactile stimuli (Buchholz et al., 2011, 2013, 2014).

To visualize individual power peaks in the frequency spectrum, spectral estimations for the 500 ms baseline intervals were calculated with a zero-padding of 10 s, allowing us to estimate spectral power in steps of 0.1 Hz (Figs. 2A–C). Alpha- and beta-band activity were defined here as 8–12 Hz and 16–24 Hz. Alpha-band selection was validated by visually inspecting individual peak frequencies. Previous studies have reported that alpha-band activity is, in general, considerably reduced in congenitally blind participants compared to sighted participants (Birbaumer, 1971; Kriegseis et al., 2006; Noebels et al., 1978; Novikova, 1973). Therefore, we first analyzed the raw power of task-unrelated oscillatory activity by comparing activity before cue-onset (500 to 0 ms pre-cue) between sighted and blind participants. Power values were separately averaged for the four clusters of interest (Figs. 4 & 6; pooled over ipsi- and contralateral hemispheres) and posture (uncrossed and crossed hands) and across the alpha- and the beta-range (8–12 and 16–24 Hz frequency bins, respectively). Separate ANOVAs for repeated measures were calculated for each frequency band with the between factor Group (sighted vs. blind individuals), and the between factor Cluster (frontal, central, parietal, parieto-occipital).

To explore task-related changes of oscillatory power, we log<sub>10</sub>-transformed power related to directing attention to the



**Fig. 2.** Spectral power during baseline. Activity between trials, A, in the sighted and, B, in the congenitally blind group averaged across electrodes within frontal, central, parietal, and parieto-occipital clusters (from top to bottom electrodes marked on the topography plot in C) and across hand postures. Thin colored lines represent individual participants; thick black line represents the group mean. Scale differs between groups. C, Mean activity in the same clusters in the sighted (blue) and in the congenitally blind (red) group. Shaded areas mark the standard error of the mean. Asterisk marks a significant difference between groups in the sensor level analysis. D, Source reconstruction of group differences in alpha-band activity. Areas with significant differences between groups are shown in opaque red (cluster-based permutation test:  $p = 0.038$ ).

hand and selected the time bin at 750 ms after the auditory cue, which corresponds to the time window 500–1000 ms after the auditory cue (that is, 500–0 ms preceding tactile stimulus onset). This choice of time window ascertained that no post-stimulus activity contributed to the analysis. Lateralization of alpha- and beta-band oscillatory activity related to anticipation of tactile stimulation has been reported to be maximal in this time range (Van Ede et al., 2012). Power estimates in the 500 ms before auditory cue onset served as baseline.

To investigate the lateralization of the alpha- (8–12 Hz) and beta-band (16–24 Hz),  $\log_{10}$ -power values were aggregated over participants and conditions and analyzed with separate ANOVAs with between subjects factor Group (sighted vs. blind individuals), and three within-subjects factors Posture (uncrossed vs. crossed), Cluster (frontal, central, parietal, parieto-occipital), and Hemisphere (contra- vs. ipsilateral relative to the attended hand). Violations of the assumption of sphericity were compensated for by adjusting the degrees of freedom using the method of Huynh and Feldt (Huynh and Feldt, 1976); we report the original degrees of freedom with corrected  $p$ -values.

#### *Correlation of behavior and EEG data*

To relate behavior to electrophysiological signals, Spearman's rho was computed between individual  $d'$  scores for target responses and the activity differences between contra- and ipsilateral electrodes during the time window of the sensor level analysis (500 to 1000 ms post-cue). Correlation coefficients were computed separately for each group, and converted into  $t$ -statistics for the purpose of multiple comparison correction using a cluster-based permutation test (CBPT, Maris and Oostenveld, 2007). In the sighted group, a prior analysis (Röder et al., 2008) had revealed a modulation of  $d'$ -scores by hand posture (see Results), precluding an analysis of behavior–neurophysiology correlations pooled over postures. Therefore, a cluster-based permutation test was run separately for uncrossed and crossed postures. In the blind group, posture did not modulate behavior or lateralization of oscillatory activity. Therefore, the correlation of  $d'$ -scores and oscillatory activity was computed pooled across postures. We note that, due to the nature of the paradigm, the trials from which  $d'$  was derived (target trials), were distinct from the trials used for EEG analysis (non-target trials).

#### *Source reconstruction*

To reconstruct the neuronal sources of alpha- and beta-band activity, we applied a beamforming technique, termed Dynamic Imaging of Coherent Sources, in the frequency domain (Gross et al., 2001; Liljeström et al., 2005). For this approach, grid points were evenly distributed along a 7 mm grid throughout the brain, and an adaptive spatial filter was used, which passes activity at each grid point, while suppressing activity from all other locations (Van Veen et al., 1997). A volume conduction model with three anatomically realistic layers was derived from the MNI template brain. Electrode positions for analysis were estimated by averaging measured electrode positions of three participants and aligning them to the volume conduction model using the nasion and preauricular points as references. The leadfield matrix for each grid point was calculated based on the boundary element method (Fuchs et al., 2002). The leadfield and the cross-spectral density (CSD) between all combinations of sensors at the frequency of interest were used to estimate source activity for each grid point. Computation of the CSD employed the Fourier approach, using a Hanning taper for the alpha-band (10 Hz  $\pm$  2 Hz) and a multitaper FFT approach using Slepian tapers the beta-band (20 Hz  $\pm$  4 Hz, 3 tapers). In equivalence with the sensor level analysis, we selected a 500 ms baseline period, centered on 250 ms preceding the auditory cue, and a 500 ms time windows in the cue–target interval, centered on 750 ms post-cue, for each participant and condition. For the localization of group differences in the alpha-band during the baseline period, estimates were

averaged across conditions and entered in a cluster-based permutation test that controls for multiple comparisons (Maris and Oostenveld, 2007) using independent  $t$ -statistics to select voxels for clustering. For the analysis of the cue–target interval, the power change for each grid point between baseline activity and post-cue activity was decibel scaled [ $P = 10 * (\log_{10}(P_{\text{postcue}}) - \log_{10}(P_{\text{baseline}}))$ ]. The lateralization of oscillatory activity was assessed by subtracting the power of ipsilateral from that of contralateral grid points relative to the attended hand. In the sighted group, after identifying an interaction effect in the alpha-band between Hemisphere and Posture at the sensor level, this effect was statistically tested in source space by a cluster-based permutation test (Maris and Oostenveld, 2007) using dependent  $t$ -statistics to select voxels for clustering. For all conditions in which Posture did not have a significant effect, data were pooled across postures and only the main effect of Hemisphere was tested. This was the case for alpha-band activity in the blind group and beta-band activity in both groups. However, when an interaction with Posture was present, lateralization was assessed separately for each posture by testing activity at contralateral versus ipsilateral grid points. This was the case only for alpha-band activity in the sighted group.

In a separate analysis, we used a 300 ms sliding window for source localization to allow inspecting neural sources of the crossing effect in the sighted group over time. We beamformed five time windows centered on 650, 700, 750, 800, and 850 ms. Due to the shorter time window, the frequency resolution was slightly lower (10 Hz  $\pm$  3.33 Hz) than for the analysis of the 500 ms time interval. Each time window was tested for significance with a CBPT, without correction for multiple tests.

## **Results**

### *Behavioral performance*

Posture significantly influenced behavior in the sighted group only (Fig. 7A; Group–Posture interaction:  $F(1, 22) = 5.87$ ,  $p = 0.024$ ), with higher  $d'$ -scores with uncrossed than with crossed hands ( $t(11) = 3.56$ ,  $p = 0.004$ ). In the blind group, behavior did not significantly differ between postures ( $t(11) = 0.18$ ,  $p = 0.862$ ). Furthermore, sighted participants outperformed blind participants with uncrossed hands ( $t(22) = 3.12$ ,  $p = 0.005$ ). The blind participants' performance did not significantly differ from the sighted group's performance with crossed hands ( $t(22) = 0.98$ ,  $p = 0.337$ ).

### *Absolute power in the baseline period*

Because previous studies have reported a strong reduction or even absence of alpha-band activity in congenitally blind compared to sighted individuals, we first analyzed the absolute power in the alpha- (8–12 Hz) and beta-band (16–24 Hz) range in the baseline interval at the four defined clusters of interest (Figs. 2A–C).

In the alpha-band, an ANOVA with between factor Group and within factor Cluster revealed a significant interaction of Group and Cluster ( $F(3, 66) = 11.12$ ,  $p = 0.002$ ). Although alpha-band activity appeared higher in the sighted than in the blind group at all tested electrode clusters (see Fig. 2), this difference was significant only at the parieto-occipital cluster (frontal:  $t(22) = 1.92$ ,  $p = 0.270$ ; central:  $t(22) = 2.37$ ,  $p = 0.108$ ; parietal:  $t(22) = 2.37$ ,  $p = 0.108$ ; parieto-occipital:  $t(22) = 3.28$ ,  $p = 0.014$ ; all  $p$ -values Bonferroni corrected). Visual inspection of Figs. 2A,B reveals that the peak of alpha-band activity, if it could be determined, was in the range of 8–12 Hz for most participants in both groups. However, a peak was not discernible for all participants as has been reported previously (Haegens et al., 2014), and this was the case more often in the blind ( $n = 2$ ) than in the sighted group ( $n = 1$ ).

In contrast to the alpha-band, we did not observe any significant differences in the baseline activity between groups for beta-band

activity (main effect Group:  $F(1, 22) = 2.32, p = 0.141$ ; main effect of cluster ( $F(3, 66) = 3.54, p = 0.068$ ; interaction of Group and Cluster:  $F(3, 66) = 1.82, p = 0.191$ ).

In line with sensor-level analysis, reconstruction of the neural sources of alpha-band activity yielded higher activity in posterior parietal areas in the sighted than in the blind group (Fig. 2D, cluster-based permutation test:  $p = 0.027$ , MNI coordinate with largest absolute t-value: 29, -92, -4). In sum, we observed a general decrease of posterior alpha-band activity in the congenitally blind compared to the sighted group.

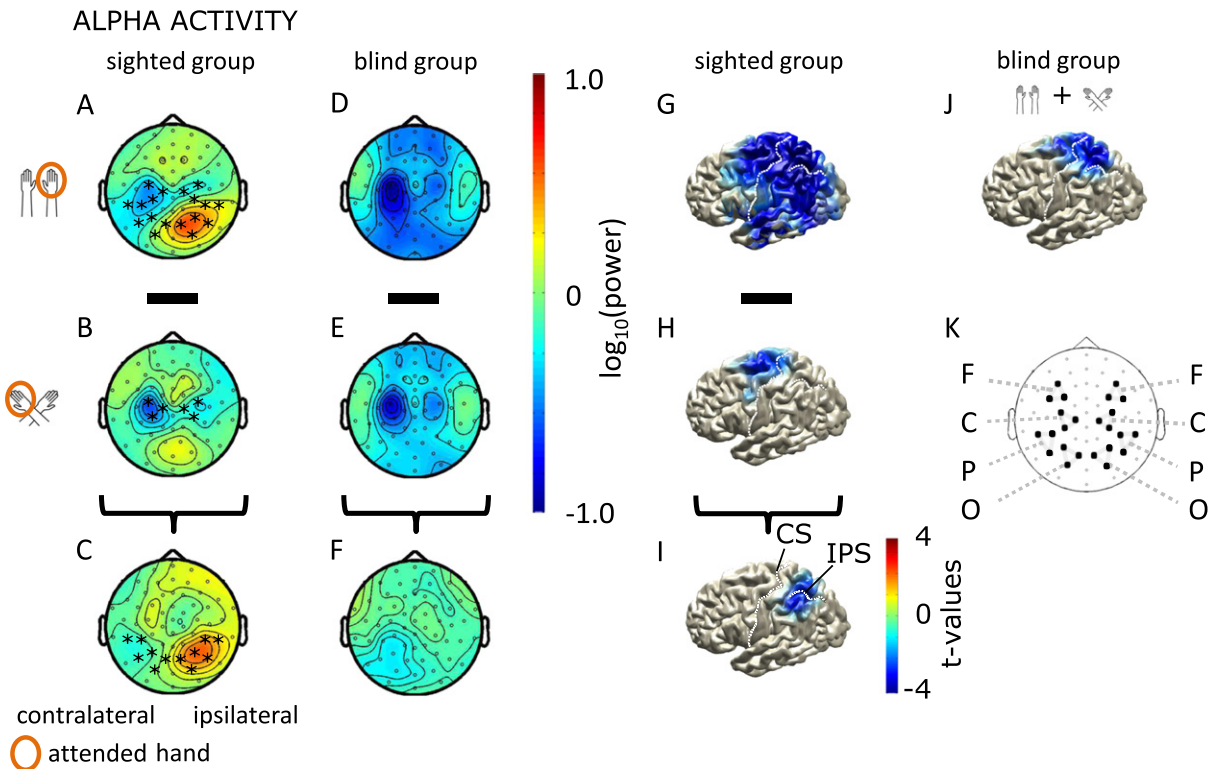
*Modulation of alpha-band activity by tactile attention*

Baseline corrected oscillatory brain activity in the alpha- and beta-band frequency ranges during the interval in which sighted and blind participants directed attention to one hand (500–1000 ms post-cue) and held their hands either in an uncrossed or crossed posture, were separately analyzed. An interaction of the factors Hemisphere and Posture would indicate that attentional orienting is modulated by hand posture and would, therefore, suggest that the use of external coordinates is associated with oscillatory brain activity. In contrast, a main effect of Hemisphere without an interaction of Hemisphere and Posture would suggest that only anatomical coordinates were relevant for the observed activity.

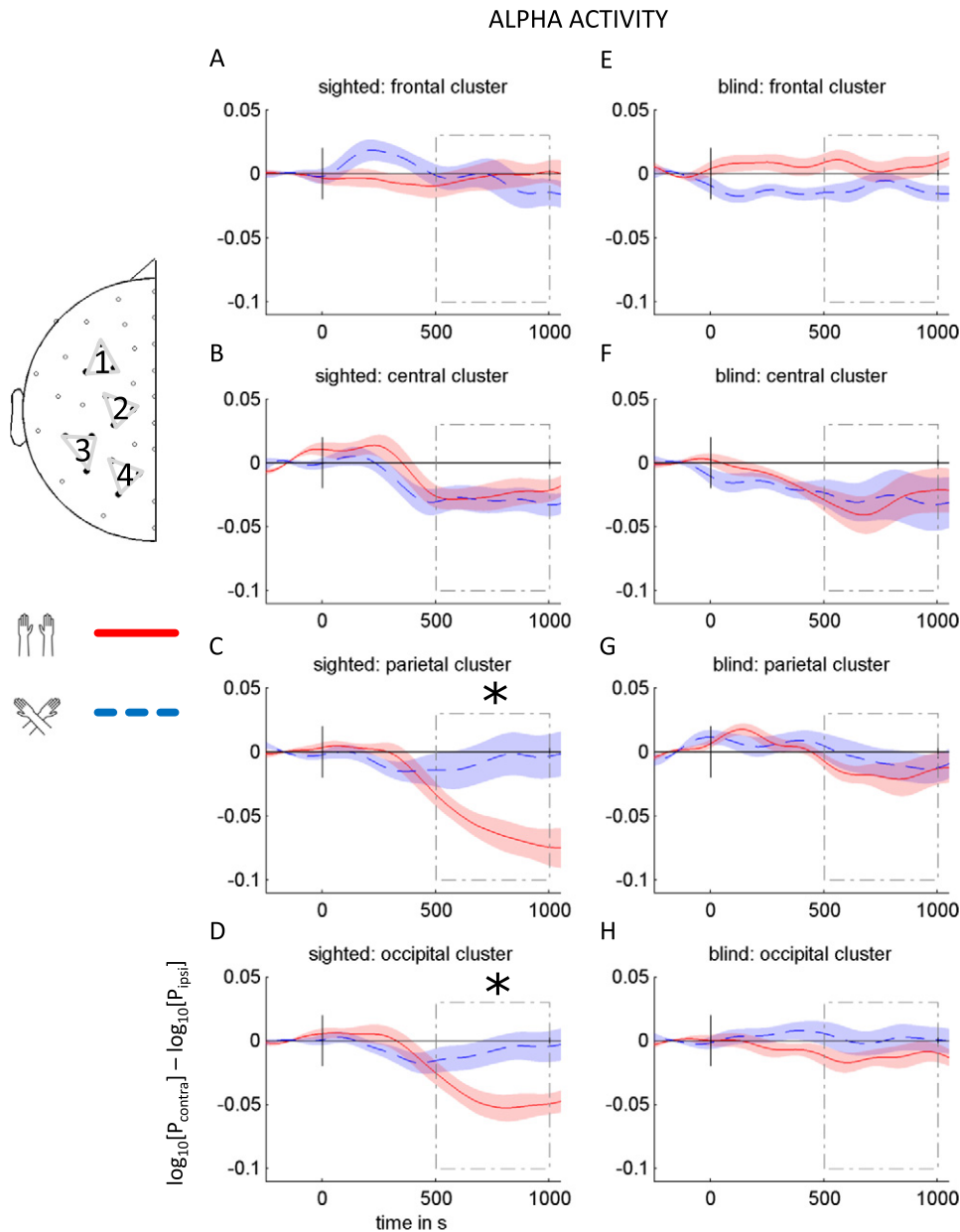
In the alpha-band frequency range (Figs. 3 & 4) an ANOVA with factors Group, Posture, Cluster, and Hemisphere revealed a trend for a 4-way interaction ( $F(3, 66) = 2.64, p = 0.069$ ) and significant 3-way interactions of Group, Posture and Hemisphere ( $F(1, 22) = 4.49, p =$

$0.045$ ), of Group, Posture and Cluster ( $F(3, 66) = 2.29, p = 0.044$ ) and of Posture, Cluster and Hemisphere ( $F(3, 66) = 5.00, p = 0.003$ ). To explore these interactions further, we analyzed each participant group separately. In the sighted group (Figs. 3 A, C, F & 4 left column), the ANOVA with factors Cluster, Posture, and Hemisphere revealed a 3-way interaction ( $F(3, 33) = 6.58, p = 0.001$ ). We further split up the analysis into separate 2-way ANOVAs with factors Posture and Hemisphere for each cluster. For the parietal and the parieto-occipital clusters (Figs. 4 C, D), Hemisphere interacted with Posture ( $F(1, 11) = 16.90, p = 0.002$ ;  $F(1, 11) = 11.43, p = 0.006$ , respectively). A main effect of Hemisphere was observed for the central cluster (Fig. 4 B) ( $F(1, 11) = 11.12, p = 0.007$ ), with a stronger alpha-band decrease contralateral than ipsilateral relative to the attended hand. Post-hoc t-tests revealed that alpha-band activity at the parietal and parieto-occipital clusters was lower in the contralateral hemisphere than in the ipsilateral hemisphere with uncrossed hands (both  $t(11) \leq -5.11, p < 0.001$ ), but did not differ between hemispheres with crossed hands (both  $t(11) \geq -0.73, p \geq 0.479$ ). Lateralization did not differ across postures for the central cluster ( $F < 1$ ). No effects were observed for the frontal cluster (Fig. 4 A, all  $F < 1$ ).

In contrast to the sighted group, for the blind group (Figs. 3 D–F, Fig. 4 right column) the ANOVA with factors Cluster, Posture, and Hemisphere revealed only a main effect of Cluster ( $F(3,33) = 5.48, p = 0.007$ ), with lower alpha-band activity at the central cluster than in the other clusters (central vs. frontal:  $t(11) = -3.01, p = 0.012$ ; central vs. parietal:  $t(11) = -2.89, p = 0.015$ ; trend for central vs. parieto-occipital:  $t(11) = -2.16, p = 0.054$ ), indicating that the modulation of alpha-band was strongest at central sites in the blind



**Fig. 3.** Alpha-band activity during the cue–target interval. A–D. Alpha-band (8–12 Hz) activity relative to baseline 500 to 1000 ms following the auditory cue, A, D, with uncrossed and, B, E, crossed hands, A–C, in the sighted and, D–F, in the blind group. C, F. Topography of the difference in the alpha-band power for uncrossed minus crossed hands postures, C, in the sighted and, F, blind groups in the same time window. The left hemisphere is contralateral to the attended hand (orange circle, see text for details). A, B, Asterisks mark electrodes within clusters showing significant lateralization of activity, A, with uncrossed and, B, crossed hands. C, Asterisks mark electrodes at which posture significantly modulated this lateralization of activity. G–J. Source reconstruction of alpha-band lateralization (i.e. contra- minus ipsilateral activity,  $t = 750$  ms post-cue) in the sighted group, G, with uncrossed hands; H, with crossed hands; I, of the difference between uncrossed and crossed postures. J, source reconstruction of alpha-band activity in the blind group. Activity was pooled across postures, because posture did not significantly modulate alpha-band lateralization. G–J, Statistically significant clusters (G, H, J) and clusters showing a trend for statistical significance (I) are shown in opaque blue. Dashed lines mark the central sulcus (CS) and the intraparietal sulcus (IPS). K. Electrode positions (black filled dots) of frontal (F), central (C), parietal (P), and parieto-occipital (O) clusters (gray triangles) used for statistical analysis at the sensor level for both alpha- and beta-band activity.



**Fig. 4.** Alpha-band (8–12 Hz) lateralization over time. Analyzed electrode clusters of interest are marked with triangles on the semi-head montage, black dots mark included channels, see text for details. The difference between contralateral minus ipsilateral (relative to attended hand) log-power over time is shown for uncrossed (solid red) and crossed (dashed blue) posture in sighted (left) and blind (right) participants. The shaded area represents the standard error of the mean. Gray boxes (dashed-dotted) mark the analyzed time window. The auditory cue was presented at  $t = 0$ . Asterisks mark electrodes within clusters at which alpha-band lateralization significantly differed between uncrossed and crossed hand postures.

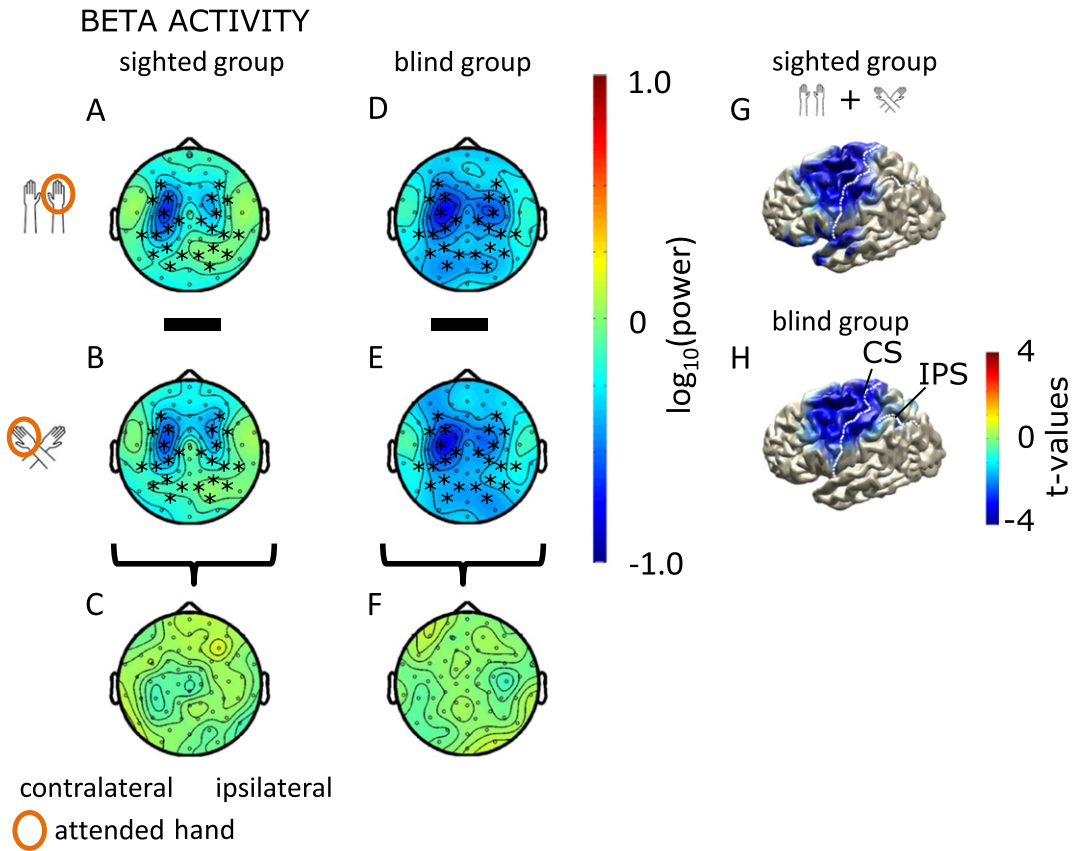
group. Moreover, activity was lower at the parieto-occipital cluster than at the parietal cluster ( $t(11) = 2.57$ ,  $p = 0.026$ ), but not compared to the frontal cluster ( $t(11) = -0.79$ ,  $p = 0.448$ ). There was a main effect of Posture, with lower alpha-band activity in the uncrossed compared to the crossed posture ( $F(1, 11) = 8.30$ ,  $p = 0.015$ ). Furthermore, we observed a trend of Hemisphere ( $F(1, 11) = 3.50$ ,  $p = 0.088$ ) with lower activity in the contralateral as compared to the ipsilateral hemisphere.

For comparison with previous studies (Buchholz et al., 2011, 2013), alpha- and beta-band activity were additionally compared for the right vs. the left hand (rather than, as here, the contra- vs. ipsilateral hand, see Fig. S1A–I). Consistent with the results presented here, the contrast of alpha-band activity between hands (Fig. S1G,H) was modulated by hand posture in the sighted group (Fig. S1, left column), but not in the blind group (Fig. S1, right column).

In sum, the sensor level analysis of alpha-band activity showed that posture significantly attenuated lateralization of posterior parietal alpha-band activity in the sighted group, whereas alpha-band lateralization at central electrodes did not significantly change across postures. In contrast, in the blind group, only a trend for alpha-band lateralization was observed, which was not significantly modulated by posture.

#### Modulation of beta-band activity by tactile attention

Analysis of the beta-band (Figs. 5 & 6) did not reveal any significant effects involving the factor Group. Beta-band activity was lower in the contralateral than in the ipsilateral hemisphere ( $F(1,22) = 23.56$ ,  $p < 0.001$ ). Importantly, beta-band activity was not significantly modulated by hand posture (main effect of Posture,  $F(1,22) = 0.11$ ,



**Fig. 5.** Beta-band activity during the cue–target interval. A–D. Beta-band (16–24 Hz) activity relative to baseline 500 to 1000 ms following the auditory cue, A, D, with uncrossed and, B, E, crossed hands, A–C, in the sighted and, D–F, in the blind group. C, F. Topography of the difference in the alpha-band power for uncrossed minus crossed hands postures, C, in the sighted and, F, blind groups in the same time window. The left hemisphere is contralateral to the attended hand (orange circle, see text for details). A, B, D, E, Asterisks mark electrodes in clusters at which activity was significantly lateralized in the sensor level analysis (see text for details). G, H. Source reconstruction of beta-band lateralization ( $t = 750$  ms post-cue), G, in the sighted and, H, in the congenitally blind group pooled across postures. Statistically significant clusters are opaque (cluster-based permutation test:  $p < 0.001$  and  $p = 0.003$ , respectively). Dashed lines mark the central sulcus (CS) and the intraparietal sulcus (IPS).

$p = 0.740$ ; all interactions with Posture:  $p \geq 0.263$ ). A comparison of activity for the left vs. right hand (rather than contra- vs. ipsilateral hand) revealed a consistent result pattern (Fig. S1R). In sum, the pattern of beta-band lateralization did not differ between sighted and congenitally blind individuals and was not significantly modulated by hand posture in both groups.

*Relation between behavior and lateralized alpha-band activity*

In the sighted group, lateralized alpha-band activity, that is, the difference in power between the two hemispheres, positively correlated with  $d'$ -scores of response accuracy at central electrodes both with uncrossed (Fig. 7B, CBPT:  $p < 0.001$ ) and with crossed hands (Fig. 7C, CBPT:  $p < 0.001$ ). Beta-band lateralization was not significantly correlated with  $d'$ -scores in the sighted group. In the blind group,  $d'$ -scores did not significantly correlate with lateralized activity in neither the alpha- nor the beta-band.

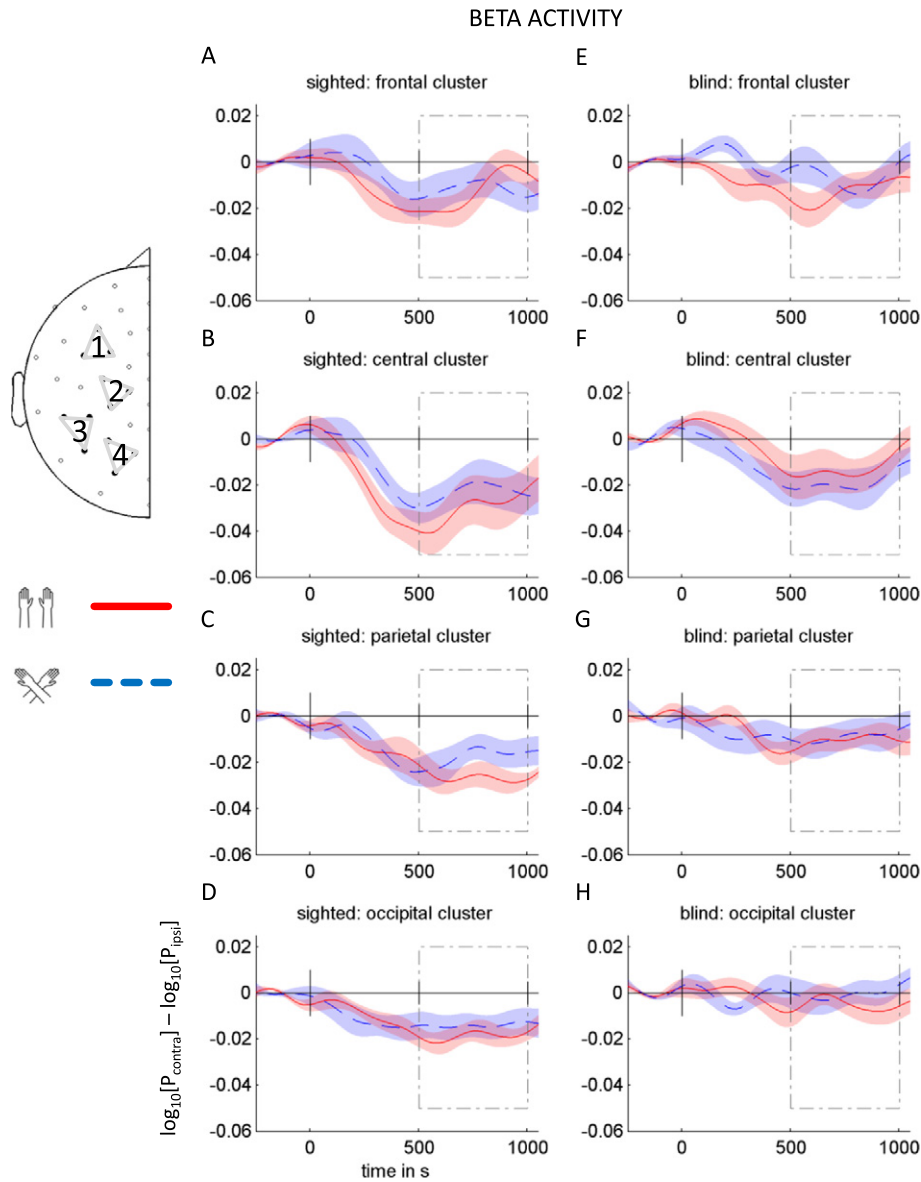
*Source reconstruction of alpha-band activity*

Source reconstruction analysis based on a beamforming approach suggested that the interaction effect of Hemisphere and Posture in the sighted group originated from the posterior parietal cortex (PPC; Fig. 3I; MNI coordinate with largest absolute  $t$ -value:  $-55, -57, 45$ ), including the intraparietal sulcus (IPS), with greater lateralization for uncrossed than crossed hands. However, this effect showed only a

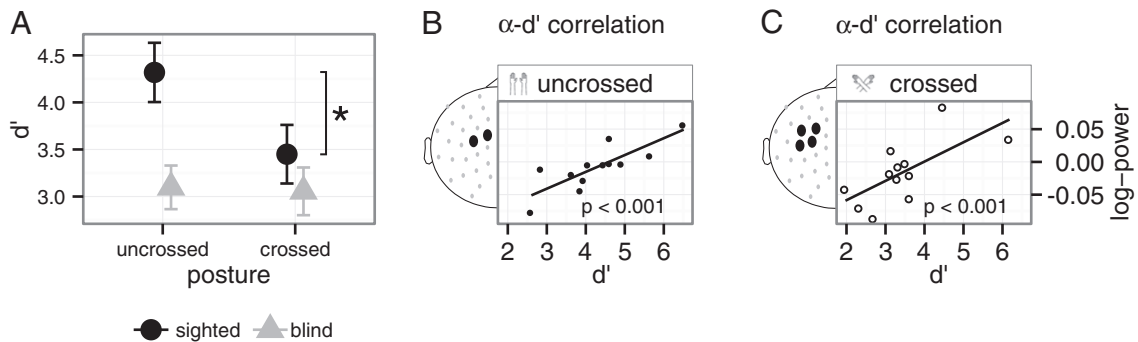
trend towards significance in source space for the selected time window (CBPT:  $p = 0.075$ ). Because there had been a significant effect on the sensor level, we further investigated this result by devising CBPT on shorter time windows (300 ms) centered on 650, 700, 750, 800, and 850 ms post-cue. This analysis rendered significant hand crossing effects on alpha-band lateralization during the time windows centered on 700, 750 and 800 ms (cluster-based permutation tests:  $p = 0.049$ ,  $p = 0.047$ ,  $p = 0.046$ , respectively) and indicated a trend during the time windows centered on 650 and 850 ms ( $p = 0.083$ ,  $p = 0.085$ , respectively). Thus, although the posture effect appeared to be similar across time, it was detectable statistically only in the middle part of the investigated time interval. Separate analyses for each posture indicated that alpha-band activity was significantly lateralized with uncrossed (Fig. 3G, CBPT:  $p = 0.004$ , MNI:  $-32, -50, 68$ ) and crossed hands (Fig. 3H, CBPT:  $p = 0.048$ , MNI:  $-34, -15, 73$ ). With uncrossed hands, alpha-band activity was lateralized over a broad area including PPC and sensorimotor areas, whereas lateralization with crossed hands was confined to peri- and precentral areas.

In stark contrast to the sighted group, but consistent with results at the sensor level, cluster-based permutation testing revealed a significant lateralization of alpha-band activity in the blind group, independent of posture, in a region including sensorimotor and posterior parietal areas (Fig. 3J, CBPT:  $p = 0.029$ , MNI coordinate with largest absolute value:  $-20, 6, 73$ ).

In sum, in accord with the results of the sensor level analysis, alpha-band lateralization in source space was observed in both sighted and



**Fig. 6.** Beta-band (16–24 Hz) lateralization over time. Figure display parallels Fig. 4. Analyzed electrode clusters of interest are marked with triangles on the semi-head montage, black dots mark included channels, see text for details. The difference between contralateral minus ipsilateral (relative to attended hand) log-power over time is shown for uncrossed (solid red) and crossed (dashed blue) posture in sighted (left) and blind (right) participants. The shaded area represents the standard error of the mean. Gray boxes (dash-dotted) mark the analyzed time window. The auditory cue was presented at  $t = 0$ .



**Fig. 7.** Behavioral results and behavior–physiology correlation. A,  $d'$ -scores in the sighted (black circles) and in the congenitally blind group (gray triangles) with uncrossed (left) and crossed hands (right). Whiskers represent the standard error of the mean. B, C. Correlation between lateralized alpha-band activity and  $d'$ -scores in the sighted group, B, with uncrossed and, C, crossed hands. In the semi-head montage, electrodes at which a significant correlation was observed are marked with black dots. Each data point represents data from one participant averaged over the marked electrodes. Least squares regression line is fitted on the depicted values. The p-value refers to the result of a cluster-based permutation test.



congenitally blind individuals. In the sighted group, the posture-related attenuation of alpha-band lateralization appeared to originate from PPC, whereas in the blind group hand posture did not significantly modulate alpha-band lateralization.

#### *Source reconstruction of beta-band activity*

Because posture did not affect beta-band activity in either group, activity was pooled over uncrossed and crossed postures for source reconstruction. Consistent with the results observed at the sensor level, we observed a significant lateralization of beta-band activity relative to the attended hand both in the sighted (Fig. 5G, CBPT:  $p < 0.001$ , MNI:  $-20, 27, 59$ ) and in the congenitally blind group (Fig. 5H, CBPT:  $p = 0.003$ , MNI:  $-6, -43, 80$ ) for central areas including M1 and S1.

## Discussion

The present study aimed at identifying the spatial reference frames underlying oscillatory activity in the alpha and beta frequency range during tactile attentional orienting, as well as the role of the visual system in establishing the neural code associated with different spatial reference frames. To this end, we compared oscillatory EEG responses in the alpha- (8–12 Hz) and beta-band (16–24 Hz) in sighted and congenitally blind adults. We dissociated signatures of anatomical and external reference frames by manipulating hand posture during a tactile spatial attention task. Oscillatory brain activity was analyzed during the attention orienting phase, that is, in the cue-stimulus interval.

We report two main results. First, in the sighted group, alpha- and beta-band activity during tactile attentional orienting were differentially affected by hand posture. Alpha-band lateralization was susceptible to hand posture over posterior parietal electrodes, with a stronger lateralization (that is, lower alpha power over the contralateral than the ipsilateral hemisphere) in the uncrossed compared to the crossed posture. In contrast, although beta- and central alpha-band activity were lateralized during attentional orienting as well (that is, decreased power contra- as compared to ipsilaterally), this lateralization depended solely on the hand to which attention was directed and was not modulated by hand posture. Second, in the congenitally blind group, alpha activity was significantly reduced as compared to sighted group. Attentional deployment in this group was accompanied by a significant lateralization of alpha- and beta-band activity relative to the stimulated hand. However, in contrast to the sighted group, the blind group's lateralization of alpha-band activity was not modulated by hand posture. Beta-band lateralization in the blind group paralleled the pattern of the sighted group and did not vary with hand posture.

#### *Tactile attention is reflected in lateralized oscillatory activity*

In sighted individuals, alpha- and beta-band activity have been associated with attentional deployment towards a specific location in space when orienting towards upcoming visual (Sauseng et al., 2005; Thut et al., 2006) and tactile events (Bauer et al., 2012; Haegens et al., 2012; Jones et al., 2010; van Ede et al., 2011). In this context, alpha-band activity has received special interest as a potential information gating mechanism. When tactile attention is oriented towards the hands, a lateralization of alpha-band activity in expectancy of tactile stimulation has commonly been observed. This lateralization is thought to reflect the allocation of attention, with lower alpha activity in the hemisphere contra- than ipsilateral to the attended hand (Anderson and Ding, 2011; Haegens et al., 2012; van Ede et al., 2011). In line with these reports, we observed both a contralateral power decrease and an ipsilateral power increase when sighted participants directed tactile attention with uncrossed hands (Fig. 3A). Like alpha activity, beta activity was lateralized during tactile attention, also with power suppression in the hemisphere contra- compared to ipsilateral to the

attended hand, a finding which is consistent with previous reports (Bauer et al., 2012; van Ede et al., 2011).

#### *External coordinates are reflected in posterior parietal alpha-band activity of the sighted*

By manipulating hand posture, we were able to define the coordinate systems relevant for the modulation of alpha- and beta-band activity. Alpha-band lateralization at posterior sites of sighted participants was attenuated when the hands were crossed. Because lateralization of oscillatory activity seems to express an attentional bias to one side, the reduction of lateralization as observed here suggests that attention deployment towards the attended hand was less specific in the crossed than in the uncrossed posture. This less specific attention deployment could lead to a behavioral disadvantage with crossed hands, and an advantage with uncrossed hands. Indeed,  $d'$  scores were highest for the uncrossed posture in sighted participants, consistent with this reasoning (Fig. 7A; Röder et al., 2008). Behavioral effects of hand crossing in studies using temporal order judgment tasks (Heed and Azañón, 2014) have been associated with the integration of conflicting information from anatomical and external reference frames with crossed hands (Heed et al., 2015). The lateralization of posterior parietal alpha-band activity could reflect either such integration of information from anatomical and external reference frames or, alternatively, the encoding of information exclusively in an external reference frame. If alpha-band lateralization reflected attention deployment exclusively in external spatial coordinates, then alpha-band lateralization should have been reversed with crossed hands. However, lateralization was merely attenuated rather than reversed. Thus, the current results suggest that both anatomical and external coordinates may modulate posterior parietal alpha-band lateralization. Such influence of several reference frames on cortical processing is in line with evidence that posterior parietal cortex encodes multiple spatial reference frames in macaques (Chen et al., 2013). The modulation of posterior parietal alpha-band lateralization we observed may therefore reflect the integration of anatomical and external information. However, the observed result pattern of reduced lateralization may, alternatively, stem from laid-over activity of central and parietal alpha sources. The spatial resolution of EEG is known to be low. It is therefore possible that the neural sources of central and parietal brain areas could not be entirely separated by the source analysis. In this case, the activity of a strong central source may have mixed with the lateralization effects at posterior parietal sites. For example, alpha-band activity acquired with MEG was reported to be differently lateralized in central versus parietal areas in expectation of the presentation of a tactile saccade target (Buchholz et al., 2014).

Whereas it remains an open question whether posterior parietal alpha-band lateralization is affected by an anatomical reference frame, the critical result of our study is that posterior parietal alpha-band lateralization definitely reflects the use of an external reference frame.

In marked contrast to posterior alpha-band activity, alpha-band lateralization at central sensors, as well as beta-band lateralization at both central and posterior parietal sensors were unaffected by hand posture, suggesting that the mechanism that is associated with central alpha- and beta-band activity operated in anatomical coordinates. These differences between frequency bands are in line with findings from several studies that have investigated tactile orienting in the context of motor planning (Buchholz et al., 2011, 2013, 2014). In these studies, participants fixated the middle finger of one hand and then saccaded (Buchholz et al., 2011) or reached (Buchholz et al., 2013) towards a tactile stimulus either at the index or at the little finger of the same hand. In this setup, the index finger of the left hand was to the right, and the little finger to the left of fixation and vice versa. Thus, with respect to gaze, touch location occurred in opposite hemifields for the two fingers, although both belonged to one body side anatomically. Alpha-band lateralization at posterior sensors depended on target position relative to gaze, implying the use of

external coordinates for tactile target representation. In contrast, alpha-band activity over central sites, as well as central and posterior beta-band activity were not modulated by gaze, and were lateralized only with respect to anatomical body side (for an analogous analysis between attentional deployment to the left and to the right hand in the current study see Supplementary Fig. S1). The close correspondence of the current results and the findings of these studies investigating attentional orienting towards motor goals may indicate that the neural mechanisms of overt and covert attentional orienting highly overlap (Baldauf et al., 2006; Corbetta et al., 1998; Deubel and Schneider, 1996; Rizzolatti et al., 1987).

Notably, individual performance for target detection correlated with alpha-band lateralization prior to stimulus presentation at central sites in standard trials in the sighted group. This correlation was evident with both uncrossed and crossed hands. Previously, it has been shown that both prestimulus alpha- and beta-band lateralization in S1 are positively related to accuracy in tactile discrimination (van Ede et al., 2012). Furthermore, entraining S1 with 10 Hz and 20 Hz TMS can lead to decreased performance in response to tactile targets at the contralateral hand (Ruzzoli and Soto-Faraco, 2014), possibly by lateralizing oscillatory activity. While the observation of a relation between  $d'$ -scores and alpha-band lateralization at central sensors is well in line with these findings, a correlation of behavior with posterior alpha- and any beta-band lateralization was not evident in the present data. It is possible that our behavioral measure was not sufficiently sensitive to uncover such a relationship. Note, that our design required behavioral localization only of deviant stimuli. We, however, analyzed oscillatory activity following standard stimuli. Though the general assumption of the adapted paradigm is that standard stimuli indicate the attentional orienting elicited by the definition of the targets (Hillyard et al., 1973), the link between behavior and neural activity is indirect in the present study. A design with behavioral responses for both target and non-target trials may be more sensitive to detect potential correlations between behavior and neural activity (van Ede et al., 2012).

#### *Neural sources of lateralized oscillatory activity*

Source reconstruction of lateralized alpha-band activity in the sighted group revealed that alpha-band lateralization in central brain areas was present with both uncrossed (Fig. 3G) and crossed hands (Fig. 3H), whereas lateralization in PPC appeared to be present only with uncrossed hands, but not with crossed hands (Fig. 3I). Furthermore, the central lateralization overlapped to a great extent with the beta-band lateralization (Fig. 5G). The presence of the central lateralization in the alpha and beta-band with both postures suggests that it reflected attentional deployment in anatomical coordinates. In line with this, TMS entrainment of the primary somatosensory cortex with 10 Hz and 20 Hz was found to lead to a decrease of performance to subsequently presented tactile targets at the contralateral hand, but not at the ipsilateral hand (Ruzzoli and Soto-Faraco, 2014).

We identified a portion of the posterior parietal cortex as the likely origin of the posture effects observed at the sensor level. In source space, the posture effect was statistically weak, and significant only for the middle of the analyzed time interval. However, the parietal region identified in the current analysis overlaps with those showing selectivity of external-spatially coded alpha-band activity during movement planning, in particular with anterior IPS activity during reach planning (Buchholz et al., 2011, 2013). Within PPC, IPS has frequently been associated with the coding of supramodal spatial maps (Cohen and Andersen, 2002; Graziano and Cooke, 2006; Schlack et al., 2005) and IPS is thought to be involved in the recoding of anatomical into external coordinates for touch (Azañón et al., 2010; Bolognini and Maravita, 2007; Renzi et al., 2013). In line with our finding of an association of posterior alpha-band activity with external coding in IPS, a study that entrained IPS with an alpha rhythm using transcranial magnetic stimulation (TMS) prior to stimulus presentation reported improved tactile

discrimination performance at the ipsilateral hand within external space relative to TMS stimulation (Ruzzoli and Soto-Faraco, 2014). Thus, this TMS effect critically depended on posture. The presumed mechanism for this effect is that TMS biased the balance of alpha-band activity towards the stimulated hemisphere (Romei et al., 2010), thus shifting tactile attention towards the corresponding side of external space (Heed, 2014). Thus, the association of parietal alpha-band activity with an external reference frame in the present study converges with the results of several studies that have investigated coordinate transformations for touch.

#### *Lateralized alpha- and beta-band activity reflect attention deployment in congenitally blind individuals independent of posture*

Developmental vision from birth seems to critically determine the use of spatial representations in touch (Collignon et al., 2009; Röder et al., 2004, 2008). The present study offers insight into the neural mechanisms that differ between sighted and congenitally blind individuals and may, thus, be at the heart of the observed behavioral differences. We observed a dissociation between sighted and blind participants in posterior alpha-band activity but not in central alpha- and in beta-band activity. In accord with previous studies using both resting conditions and different cognitive tasks, we observed a significant reduction of the overall level of alpha-band activity in parietal and occipital brain areas in congenitally blind compared to sighted individuals (Birbaumer, 1971; Kriegseis et al., 2006; Noebels et al., 1978; Novikova, 1973).

The fact that posterior parietal alpha-band activity is associated with external coordinates in the sighted suggests that automatic external-spatial processing is closely related to the alpha frequency band. At the sensor level, the congenitally blind group only showed a trend for significant attention-related alpha-band lateralization even with uncrossed hands both at posterior parietal and central sites. At the source level, however, alpha-band activity was significantly lateralized in an area ranging from somatosensory regions to posterior parietal cortex (Fig. 3J). This indicates a possible role of these brain regions during attention deployment even in the absence of developmental vision. In contrast to the sighted group, this lateralization was not significantly modulated by posture in the blind group, possibly relating to the behavioral results that remained unchanged across postures for this group as well (Fig. 7A). Furthermore, the fact that the lateralization was not significantly modulated by posture suggests that the overall modulation of alpha-band activity by hand posture in the blind group, evident in a main effect of Posture across all sensors, reflects a modification of brain function that is not related to external spatial processing. Instead, this effect must reflect a more general, non-spatial aspect of the task, as for example that holding the hands in a crossed posture is more demanding than in an uncrossed posture. Furthermore, we did not observe any significant correlation between lateralized activity and behavior in the blind group. This finding suggests that alpha-band lateralization during tactile attention deployment is linked to behavioral responses through different mechanisms in sighted and blind individuals.

The apparent lack of the use of external coordinates during tactile attentional orienting in congenitally blind humans corroborates previous evidence suggesting that the absence of vision from birth significantly changes tactile spatial processing (Röder et al., 2004, 2008). Although congenitally blind individuals can make use of an external reference frame when task instructions suggest or require its use (Eardley and van Velzen, 2011; Heed and Röder, 2014; Röder et al., 2007), they appear to rely on an anatomical reference frame otherwise, as in the current study.

The neural structures thought to generate oscillatory alpha-band activity (Lopes da Silva et al., 1973, 1980; Lőrincz et al., 2009), including the visual thalamus as well as the lower layers of the visual cortex, have been found to be atrophied in congenitally blind individuals (Pfitzner et al., 2008; Shimony et al., 2006). We speculate that full functionality of the neural mechanisms underlying posterior alpha-band may be a prerequisite of the preferred use of external coding of sensory events.

Thus, the lack of external coding in congenitally blind individuals may be a consequence of the reduced posterior alpha system. This lack may lead, in turn, to impaired multisensory interactions based on spatial location in congenitally blind individuals (Collignon et al., 2009; Hötting et al., 2004; Ocelli et al., 2012).

#### *Attention-related beta-band activity is lateralized similarly in congenitally blind and sighted individuals*

In both sighted and blind groups, beta-band activity was lateralized following the attentional cue, with lower activity over the contra- than the ipsilateral hemisphere. In both groups, this lateralization was unaffected by hand posture. This finding suggests that the process which elicits anatomically coded activity in the beta range is similarly implemented in tactile attention-related processing in the two groups, and, consequently, that these processes are independent of developmental vision.

In summary, whereas posterior parietal alpha-band activity appears to play a role in external coding of tactile stimuli in sighted individuals, central alpha- and beta-band oscillatory activity rather reflect anatomical coordinates for tactile attention in both sighted and blind individuals. Developmental vision seems to be crucial for setting up the neural structures generating posterior alpha-band oscillations. Their lack may be the neural correlate of why a default external coding of touch is not observed in the absence of vision from birth.

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#### **Conflict of interest**

There is no conflict of interest.

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