

## 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

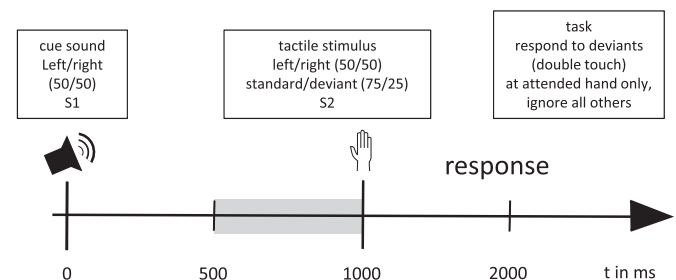
Continuous EEG data was recorded from 61 equidistantly arranged scalp electrodes. The sampling rate was 500 Hz with an analog passband filter of 0.1–100 Hz of the amplifiers (Synamps, Neuroscan). To monitor eye movements, additional electrodes were placed near the outer canthi of the eyes and under the 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).

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