

Spatial processing of touch in sighted and congenitally blind humans

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Abbreviations

ANOVA analysis of variance
BOLD blood oxygenation level–dependent
CBPT cluster-based permutation test
CS central sulcus
EEG electroencephalography
ERP event-related potentials
fMRI functional magnetic resonance imaging
GLMM generalized linear mixed model
IPS intraparietal sulcus
LMM linear mixed model
MEG magnetoencephalography
PPC posterior-parietal cortex
RT reaction time
S1 primary somatosensory cortex
SC superior colliculus
TMS transcranial magnetic stimulation
TOJ temporal order judgement

Chapter 1: Summary

We easily interact with our environment in daily life. For instance, when an object touches our hands, we can quickly localize it and look at it for further exploration. This seemingly effortless act poses a remarkable challenge for the brain. The tactile information about skin location on the hand is, yet, not enough to localize the origin of the tactile event in external three-dimensional space, because the hand could be anywhere around the body, for example, in front of the body or behind the back. Thus, to successfully localize touch the brain needs to integrate somatosensory skin-based information and posture-related proprioceptive, visual, and vestibular information about body parts. Yet, despite a large body of research we do not know exactly how the brain integrates such multisensory information for tactile localization. Here, I approach this question in several ways. The thesis begins with a general overview about how the brain may integrate signals coming from multiple senses to construct a coherent percept of the world (Chapter 2). Then, a description of how multisensory integration contributes to tactile localization follows, together with background information on the specific hypotheses of the present studies (Chapter 2, Section 2.2-2.7). Subsequently, I provide a detailed description of the conducted studies (Chapters 3–6) and end with concluding the thesis in a general discussion of the reported findings (Chapter 7).

Touch can be represented relative to an anatomical skin-based reference frame and, after integration with posture, relative to an external spatial reference frame. Sighted humans are thought to automatically integrate information coming from anatomical and external spatial reference frames, whereas congenitally blind humans do not appear to integrate external spatial information by default, indicating a critical involvement of developmental vision. Yet, the temporal dynamics of the underlying neural correlates of this differential spatial encoding in these two populations are largely unknown. In the **first study** (Chapters 3 & 4), I investigated how oscillatory brain activity reflects this differential spatial encoding. To this end, the electroencephalogram was recorded while sighted and congenitally blind participants were cued to attend to one hand to detect rare tactile deviant stimuli while ignoring deviants at the other hand as well as tactile standard stimuli at both hands. In each trial, an auditory cue instructed participants to direct attention to one hand, and a tactile stimulus was subsequently presented either to the attended or to the unattended hand. Participants adopted either an uncrossed or

crossed hands posture to probe spatial reference frames. Critically, with crossed hands anatomical and external spatial reference frames were misaligned with the left hand occupying the right external space and vice versa.

In the cue-target interval (Chapter 3), oscillatory alpha- and beta-band activity of sighted participants was lateralized with uncrossed hands over parietal and central somatosensory areas, with lower activity in the contralateral than in the ipsilateral hemisphere relative to the attended hand. Hand crossing selectively attenuated the degree of posterior-parietal alpha-lateralization, indicating that external spatial coordinates affected attentional orienting. In contrast, cue-related lateralization of central alpha-activity as well as of beta-activity was unaffected by hand crossing, suggesting that these oscillations exclusively encoded anatomical coordinates. In congenitally blind participants, central alpha-band activity was lateralized, but did not significantly change with hand postures. The pattern of beta-band lateralization was indistinguishable between groups.

During tactile stimulus processing (Chapter 4), attended compared to unattended standard stimuli suppressed alpha- and beta- bands activity of sighted participants over ipsilateral centro-parietal and occipital cortex. Hand crossing attenuated this attentional modulation selectively in the alpha-band range, predominantly over ipsilateral posterior-parietal cortex. In contrast, although contralateral alpha- and beta-activity were enhanced for attended versus unattended stimuli in blind participants, hand posture did not significantly modulate oscillatory activity. Together, the **first study**'s findings (Chapters 3 & 4) suggest that oscillatory alpha-band activity reflects external coding in sighted individuals during both attentional orienting and stimulus processing. Congenital blindness markedly alters tactile spatial coding, and, as found here, also the pattern of alpha-band activity. Because the neural mechanisms for posterior alpha-band generation appears to be linked to developmental vision, the lack of this neural mechanism in blind individuals may be related to their absence of a default integration of external spatial information in tactile processing.

In a **second study** (Chapter 5), I tested whether task demands modulate tactile localization in sighted and congenitally blind individuals. In sighted individuals, task demands, such as instruction and frequency of posture change, are known to modulate the integration of anatomical and external spatial information for tactile localization. These context

effects appear to arise from weight adjustments for the spatial integration of skin-based and external, posture-related information. In contrast, congenitally blind humans were long thought to rely exclusively on skin-based information when localizing touch and, thus, to refrain from automatic spatial integration. Accordingly, task context should not affect blind participants' tactile localization performance. To test this hypothesis sighted and congenitally blind participants localized tactile targets on the palm or back of one hand, while ignoring simultaneous tactile distractors at congruent or incongruent locations on the other hand. Hand posture was varied, either blockwise or trial-by-trial, to probe the interplay of anatomical and external location codes for spatial congruency effects: either both palms faced down, or one faced down and one up. In the latter posture, externally congruent target and distractor locations (both up/down) were anatomically incongruent (palm and back of the hand). Target locations had to be reported either anatomically ("palm" or "back" of the hand), or externally ("up" or "down" in space). Under anatomical instruction, performance was better following anatomically congruent than incongruent target-distractor pairs. In contrast, under external instruction, performance was best when target-distractor pairs were externally congruent. These congruency effect modulations were comparable in sighted and blind individuals, although effects were smaller in the latter group. Whether posture varied blockwise or trial-by-trial did not significantly modulate congruency effects. These results suggest that blind individuals, like sighted persons, automatically integrate anatomical and external information during tactile localization, and that integration is modulated by task context. Thus, the integration of anatomical and external spatial information in tactile processing is flexible and strategic even in the absence of developmental vision.

Finally, spatial information for tactile localization is not integrated for the sake of tactile localization itself, but to enable motor actions towards events in the environment. In the visual system, saccade planning has been tightly linked to shifts of spatial attention to the saccade goal. Whereas goal-directed manual motor planning appears to similarly shift visual spatial attention towards the movement goal, evidence is scarce that links shifts in tactile spatial attention to goal-directed movement planning with effectors other than the eye. In a **third study** (Chapter 6), I, thus, hypothesized that movement planning

to point with the nose to one of the hands would enhance tactile processing at the goal hand compared to the non-goal hand. In three paradigms, a tactile stimulus was presented at one of the hands while participants prepared a pointing movement with the nose to one of their hands to assess tactile processing at the movement goal (Experiments 6.1, 6.2, 6.3a) or with the hands to the nose to assess processing at the effector (Experiment 6.3b). The electroencephalogram (Experiment 6.1) and behavioral discrimination performance (Experiments 6.2 & 6.3) in response to tactile stimulation were analyzed. Moreover, if goal-directed movement planning shifted tactile spatial attention, then it is not clear whether these shifts take place relative to skin-based anatomical space or relative to external space. In order to probe this question participants held their hands either in an uncrossed or crossed posture in all experiments.

The findings did not lend strong support to the idea that movement planning with the head or the hand shifts tactile spatial attention towards the movement goal or the effector, respectively. Specifically, the pattern and the timing of movement planning related effects on somatosensory event-related potentials contrasted previous reports on covert tactile attention (Experiment 6.1). In addition, tactile discrimination performance was only marginally affected by movement planning (Experiments 6.2 & 6.3). Because no significant movement planning effects were observed that could be related to spatial attention shifts, it was, in turn, not possible to observe modulations by spatial reference frames. Movement planning effects have been frequently observed for eye movement planning on visual, tactile, and auditory stimulus processing at the saccade goal and for manual movements on visual stimulus processing at the movement goal. Yet, the absence of movement planning effects, suggests that movement planning may not generalize from the visual system to all effectors and all modalities.

To summarize, the current thesis suggests four conclusions: First, oscillatory alpha-band activity plays a pivotal role of in the coding of external spatial information for touch. Second, the implementation of oscillatory alpha-band activity for such coding critically depends on developmental vision. Alpha-band activity, thus, appears to relate to differential integration of external spatial information for touch, which has often been reported to be integrated by default in sighted, but not in congenitally blind individuals. Third, the weighting of anatomical and

external spatial information for tactile localization is flexible and strategic in both the presence and absence of developmental vision, even though one may have speculated that external spatial information is not integrated in the absence of developmental vision. Fourth, contrary to the tight link between motor planning in the visual system and spatial attentional mechanisms, the relation between covert tactile spatial attention and goal-directed movement planning with the head and hand appears to be weak or even absent.

In conclusion, the present thesis adds to our understanding of how the brain integrates the multitude of sensory information it is exposed to at every moment. Both sensory experiences during ontogeny and current task demands influence the integration of the available sensory information. Oscillatory brain activity appears to be one of the underlying neural mechanisms allowing the brain to orchestrate this integration in a flexible fashion. A flexible integration is highly beneficial to be able to smoothly respond to the permanently changing environment.

Chapter 2: Introduction

We interact smoothly with our environment in our daily life. Even though we are exposed to a multitude of information at every moment, it is usually not a problem for us to make sense of the incoming information and to construct a coherent percept of the world. For instance, we can effortlessly tell whether the touch we just felt on the hand originated from being touched by the cat sitting on our lap or by the dog sneaking around our legs, although the tactile sensation on the skin might have been very similar. In order to correctly attribute the touch to the cat or to the dog, we need to know where in space our hand is. Thus, to localize touch in space our brain needs to integrate somatosensory information with information coming from other sensory modalities, such as visual, vestibular, kinesthetic, and proprioceptive information. The question is how exactly does the brain manage to integrate information arriving via different sensory channels? This has inspired research in many different academic disciplines in the past (for overviews see Bremner, Lewkowicz, & Spence, 2012; Murray & Wallace, 2012; Stein, 2012b).

In the following, I will outline what we know from previous literature about how the brain integrates such *multisensory* information. In my thesis, I investigate tactile localization, which requires multisensory integration. Subsequently to the general introduction, I will outline why tactile localization requires the integration of multisensory information and what we know about the processes and factors that contribute to this integration. Consequently, I identify open questions that I address in the present thesis.

2.1 Multisensory integration

Many regions of the human brain are considered to be multisensory. That is, they respond to sensory information from more than one modality and to combinations of sensory information. Such areas include subcortical structures and primary sensory cortices, which have traditionally been regarded to encode only one sensory modality (e.g., Calvert & Thesen, 2004; Driver & Noesselt, 2008; Falchier, Cappe, Barone, & Schroeder, 2012; Murray et al., 2016; Schroeder & Foxe, 2005). For instance, it has been recently argued that the primary visual cortex is essentially multisensory (Murray et al., 2016). In fact, it has even been proposed that the whole neocortex may be multisensory (Ghazanfar & Schroeder, 2006). Thus, a widespread brain network appears to be involved in the integration of multisensory information.

Why is multisensory integration advantageous for perception? Encoding multisensory information allows the perception of qualities of the world distinct to one modality. For instance, pitch perception is unique to audition and color perception unique to vision. At the same time, *supramodal* information, such as spatial and temporal information, can be encoded in more than one modality and, thus, provide redundant information (Spence, 2012; Stein & Meredith, 1993). Combining redundant spatial and temporal information can be of critical importance in daily life, for example, localizing an approaching car by combining visual and auditory information, and has frequently been shown to enhance perceptual responses in human observers: Specifically, stimulation of two sensory modalities, that is, bimodal stimulation, at approximately the same location and time leads to higher stimulus detection rates and to faster and more accurate responses than unimodal stimulation (e.g., Frassinetti, Bolognini, & Làdavas, 2002; Frens, Van Opstal, & Van der Willigen, 1995; Harrington & Peck, 1998; Hershenson, 1962; Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994; Lovelace, Stein, & Wallace, 2003; Stein, Meredith, Huneycutt, & McDade, 1989; Stein, Scott Huneycutt, & Alex Meredith, 1988). In addition, the combination of redundant information is reflected in both enhanced and decreased single cell responses in the mammalian brain, originally measured in the cat's superior colliculus (SC): Some multisensory SC neurons dramatically increase their firing rate in response to bimodal audio-visual stimuli compared with firing rates in response to unisensory visual or unisensory auditory stimuli (Meredith & Stein, 1983). This increase in firing rate can even be larger than the sum of unisensory firing rates combined (Meredith & Stein, 1983). Other SC neurons show a response depression with decreased firing rates following bimodal stimulation compared to unisensory stimulation (Meredith & Stein, 1983). Based on how SC cells responded to temporal and spatial correspondences across multisensory inputs, the *temporal* and the *spatial principle*, that are fundamental for multisensory integration, were derived (Meredith & Stein, 1983; Stein & Stanford, 2008). The *temporal principle* predicts maximal multisensory integration when constituent stimuli in different modalities are presented at approximately the same time (King & Palmer, 1985; Meredith, Nemitz, & Stein, 1987). The *spatial principle* states that maximal multisensory integration occurs when stimuli are approximately presented at the same location (King & Palmer, 1985;

Meredith & Stein, 1986). In addition, a third principle was formulated. The *principle of inverse effectiveness* states that maximal multisensory integration occurs when at least one of the inputs is, by itself, only weakly effective in exciting a neuron (Holmes & Spence, 2005; Meredith & Stein, 1983). In short, the brain most likely integrates multisensory information that originates from the same spatial location at the same moment in time, and integration is maximal, when at least one of these inputs only weakly excites the sensory pathways.

However, stimuli in different modalities do not have to perfectly overlap in space and time to be integrated. For example, we perceive spoken words to originate from the mouth of an actor when watching a movie as opposed to perceiving sounds to originate from a loudspeaker. A strategy to quantify how much discrepancy between events in different modalities still allows multisensory integration is to systematically introduce a temporal or spatial separation between sensory events. Increasing temporal and spatial separation between multisensory signals decreases the interaction between these signals in human observers (e.g., Bertelson & Aschersleben, 2003; Morein-Zamir, Soto-Faraco, & Kingstone, 2003; Slutsky & Recanzone, 2001; Vroomen & de Gelder, 2004). The range, in which a multisensory interaction is likely to be observed has been denoted *window of multisensory integration* or *multisensory binding window* (e.g., Wallace & Stevenson, 2014). Such windows allow integrating multisensory events that are slightly discrepant in space and time. This is an advantageous feature given that discrepancies between sensory modalities occur naturally due to physical properties of the stimuli (e.g., light travels faster than sound), the sensory pathways involved (e.g., faster neural transduction times for auditory than visual inputs), and environmental (e.g., day vs. night) as well as bodily changes (e.g., growth). Thus, *windows of multisensory integration* allow the brain to adapt to the current situation and to integrate signals that are slightly discrepant in space or time.

Presenting temporally or spatially discrepant signals can also lead to illusory percepts, such as the *rubber hand illusion* or the *double-flash illusion* (Botvinick & Cohen, 1998; Shams, Kamitani, & Shimojo, 2000). In the *rubber hand illusion*, the hidden hand of a participant and a seen rubber hand are stroked in synchrony and participants regularly perceive the rubber hand to be part of their own body and localize their own hand towards the rubber hand (Botvinick & Cohen, 1998). Vision with a characteristically high spatial resolution, thus, appears to

dominate this perceptual illusion. In the *double-flash illusion*, participants erroneously report to perceive several light flashes when two or more auditory beeps are presented simultaneously with a single light flash (Shams et al., 2000). Thus, visual perception is altered by auditory input, which may be taken as evidence that the auditory modality with its relatively high temporal resolution is the modality dominating perception in this example. One explanation for the outlined illusions has been offered, such that the ‘most appropriate’ modality for the current task in a given situation dominates perception (Welch, DuttonHurt, & Warren, 1986; Welch & Warren, 1980). The modality appropriateness hypothesis, however, may constitute a somewhat vague post-hoc explanation (e.g., Alais & Burr, 2004; Spence, 2012), with scientists arguing that the ‘appropriate’ modality is the one that happened to dominate perception in a certain situation.

Computational models offer an alternative explanation to understand how the brain integrates multisensory signals and why one modality dominates perception in certain situations. They put forward the notion that the brain weights the relative contribution of each sensory input depending on its relative reliability, that is, the inverse variance (Alais & Burr, 2004; Battaglia, Jacobs, & Aslin, 2003; Ernst, 2012; Ernst & Banks, 2002; Ernst & Bühlhoff, 2004; Körding & Wolpert, 2004; Landy, Maloney, Johnston, & Young, 1995; Trommershauser, Körding, & Landy, 2011). For instance, visual signals are more reliable on a sunny day compared to a snowstorm at night, and auditory signals are more reliable when paired with silence compared to background noise. According to these models sensory signals are integrated in a *statistically optimal* fashion, where multisensory estimates are more reliable, that is, less variable, than each of the unisensory inputs (Alais & Burr, 2004; Ernst & Banks, 2002). This weighting scheme accounts well for observers’ behavioral performance when the reliability of the visual information is systematically degraded, for instance, in visual-haptic object-size estimation (Ernst & Banks, 2002), and in visual and auditory localization in the context of the audio-visual ventriloquist illusion (Alais & Burr, 2004). Not only the variance within each modality influences the joint estimation of the location (or timing) of a multisensory event, but also prior knowledge and expectations about the co-occurrence statistics in the environment (Ernst, 2012). Such a priori knowledge can be modeled as a prior probability within the Bayesian framework (Ernst, 2012). A Bayesian model, in its most basic form, estimates the value of a certain

variable (e.g., location of a stimulus) by combining information from collected sensory evidence (e.g., an audio-visual event) with prior information (e.g., expectations regarding stimulus location and signal types). In the case of multisensory perception, multiplying the weighted integration estimates with a prior probability results in a posterior distribution, which reflects not only the most probable value of the multisensory stimulus, that is, the maximum-a-posteriori estimate, but also the observers uncertainty through the width of the posterior distribution (Ernst, 2012; Ma & Pouget, 2008). Research on the neural underpinnings of multisensory integration suggest that on the neuronal level, Bayesian-optimal signal integration can be implemented via networks that linearly combine the population pattern of activity elicited by each sensory signal (Gu, Angelaki, & DeAngelis, 2008; Ma, Beck, Latham, & Pouget, 2006; Pouget, Deneve, & Duhamel, 2002). In short, the brain appears to integrate multisensory information by combining each contributing information depending on its signal variability and on prior information. Thus far some ideas of how the brain may generally combine multisensory information have been laid out. Tactile localization requires multisensory integration and will be discussed in more detail in the following.

2.2 Tactile localization requires multisensory integration

Touch is initially encoded relative to the skin in an anatomical reference frame, evident in the homuncular organization of the somatosensory cortex (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950). In order to successfully localize touch in three-dimensional space relative to an external spatial reference frame, the anatomical information needs to be integrated with visual, proprioceptive, and vestibular information (Clemens, Vrijer, Selen, Gisbergen, & Medendorp, 2011; Driver & Spence, 1998; Heed, Buchholz, Engel, & Röder, 2015; Holmes & Spence, 2004; Maravita, Spence, & Driver, 2003). Indeed, sensory information coming from multiple modalities is thought to be constantly recoded into a common external spatial reference frame to integrate multisensory information (Pouget, Ducom, Torri, & Bavelier, 2002). Several spatial reference frames have been used in the literature to describe how the brain represents spatial relationships. The important difference is the origin to which they are anchored to. An *anatomical* reference frame as described above is anchored to the skin, and is also referred to as skin-based or as somatotopic reference frame. An

external reference frame in the context of tactile localization refers to the tactile localization after information about body posture has been integrated with the skin location. Yet, such an *external* reference frame may be anchored to the eyes, head, torso, or limbs (e.g., Heed, Backhaus, Röder, & Badde, submitted; Shore, Spry, & Spence, 2002). These two reference frames, *anatomical* and *external*, are *egocentric*, meaning their origin and axis depend on the location, orientation, and posture of the subject. In contrast, an *allocentric* reference frame has its origin in the environment and is independent of the subject. For instance, the geographical coordinate system of the earth is anchored to the intersection of the Greenwich meridian and the equator, that is, 0° latitude and 0° longitude, and it is independent of the location, orientation, or posture of a subject. The brain, however, has recently been suggested to encode space relative to *egocentric* spatial reference frames only (Filimon, 2015).

As the concept of spatial reference frames for tactile processing is central to the present thesis, it is illustrated in Fig. 2.1. Tactile spatial reference frames can be investigated by manipulating the hand posture. With hands in an uncrossed posture reference frames are aligned, that is, a tactile stimulus presented to the left hand is also left relative to an external spatial reference frame (Fig. 2.1A). Crossing the hands over the midline (Fig. 2.1B) misaligns anatomical and external spatial reference frames, that is, a tactile stimulus presented to the left hand is now right relative to an external spatial reference frame. In the studies of the present thesis, head, torso, and eyes are aligned. The present studies will, thus, not differentiate between external spatial reference frames anchored to the eyes, head, or torso (Fig.2.1C).

In humans, spatial reference frames in touch have frequently been investigated using tactile temporal order judgements (TOJ; for a recent review see Heed & Azañón, 2014). In this task, participants judge the temporal order of two tactile stimuli delivered in rapid succession, one to each hand. With hands held in an uncrossed posture (Fig. 2.1A), the intervals that are necessary to correctly judge the temporal order in more than 75 % of cases are rather short, that is, 30–70 ms (Shore et al., 2002; Yamamoto & Kitazawa, 2001). With crossed compared to uncrossed hands, error rates and reaction times increase, and the intervals that are necessary to correctly judge the temporal order in more than 75 % of cases double or even triple in size, that is 120–300 ms (Shore et al., 2002; Yamamoto & Kitazawa, 2001). Critically, to solve

the task it is not necessary to take posture into account given that participants are asked to respond with the hand that has been stimulated first. The fact that one can still observe an effect of hand crossing on performance suggests an *automatic* integration of anatomical and external spatial information. Electrophysiological evidence corroborates the notion of an automatic encoding of external spatial information: Attention-related effects on somatosensory event-related potentials (ERP) between 80 and 300 ms after tactile stimulus onset have been reported to be attenuated with crossed compared to uncrossed hands (Eardley & van Velzen, 2011; Eimer, Forster, & Van Velzen, 2003; Gherri & Forster, 2012a; Heed & Röder, 2010; Röder, Föcker, Hötting, & Spence, 2008). Thus, posture-related information is automatically taken into account when processing touch.

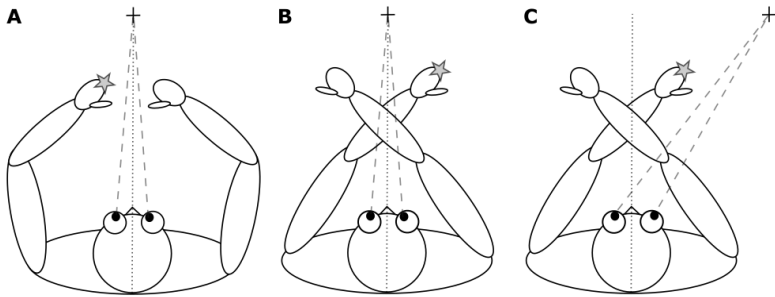


Figure 2.1. Schematic illustration of the concept of spatial reference frames for tactile localization as seen from above. **A.** Spatial reference frames are aligned with uncrossed hands. That means that a tactile stimulus at the left hand (gray star) is on the left of the body and left relative to external spatial reference frames. Gray dashed and dotted lines represent eye orientation to a fixation cross and head/body midline, respectively. **B.** Hand crossing can misalign anatomical and external spatial reference frames. Whereas a tactile stimulus at the left hand is still on the left of the body, it is on the right side relative to external spatial reference frames. Note, however, that external spatial reference frames anchored to the eyes, head, and torso are still aligned. **C.** External reference frames can be misaligned as well. In this example eye fixation is to the right side, whereas head and torso positions are unchanged compared to A and B. The tactile stimulus from the example is still on the left body side and left relative to an external eye-centered reference frame, but right relative to external reference frames anchored to the head and to the torso. More possibilities to systematically disentangle the external spatial reference frames relevant for tactile localization have been reported recently (Heed et al., submitted).

To account for the hand crossing effect in the TOJ it has recently been suggested that the initial anatomical information is, in a first step, automatically remapped into an external reference frame (Badde, Heed, & Röder, 2015). Then, in a second step, information coming from different reference frames is integrated (Badde, Heed, et al., 2015). In addition, anatomical and external spatial information are differently weighted for this integration depending on current task demands, presumably under top-down control (Badde, Heed, & Röder, 2014; Badde, Heed, et al., 2015; Badde, Röder, & Heed, 2015). Critically, the initial modality specific information is not lost after integration, but remains available (Heed, Buchholz, et al., 2015). This is in line with computational principles proposed for neural networks regarding the mediation of information encoded in different spatial reference frames (Pouget, Deneve, et al., 2002). In these networks different input layers of several neural units encode input relative to a specific reference frame, for instance, one input layer encodes the location of a visual target object relative to the eyes, and another the position of the eyes themselves (Pouget, Deneve, et al., 2002). The information coming from the input layers is then combined in an intermediate layer that contains basis function units. Each basis function unit computes the product of a pair of eye-position and eye-centered units, and, thus, responds maximally to a specific combination of eye-centered target location and eye position. An output layer then linearly combines the activities from the intermediate layer, and the activity in the output layer reflects the target position in a head-centered reference frame. Pouget and colleagues (2002) proposed that these networks are recurrently connected, allowing for bidirectional information flow. Since original and intermediate reference frame information is processed in different network layers, this model is in line with the proposal of a concurrent encoding of 'original' and integrated information (Heed, Buchholz, et al., 2015).

Several studies have provided evidence of concurrent encoding of anatomical and external spatial information. For instance, Eimer, Forster, and van Velzen (2003) investigated the spatial reference frames underlying *covert* shifts of tactile spatial attention, that is, shifting one's focus of attention towards a specific point in space without moving the eyes. They recorded the electroencephalogram (EEG) from the scalp of their participants, while participants directed their attention to one hand to detect subsequently presented rare tactile target stimuli at that

hand. In order to probe spatial reference frames the hands were either placed in an uncrossed or crossed posture (cf., Fig. 2.1A, B). They observed that lateralized EEG activity, that is, the difference between contralateral and ipsilateral activity, following a spatial cue reflected both the anatomical and the external spatial location of the attended hand. Specifically, lateralized EEG activity at posterior electrodes was related to a shift of spatial attention relative to the external spatial location of the attended hand. In contrast, lateralized EEG activity at anterior electrodes was related to a shift relative to the anatomical location of the attended hand (Eimer et al., 2003). Moreover, effects of covert spatial attention on somatosensory ERPs have been reported to be modulated by both anatomical and external spatial distance, indicating a concurrent encoding of anatomical and external spatial reference frames (Heed & Röder, 2010). In addition, oscillatory brain activity (for details see Section 2.3.3) measured with magnetoencephalography (MEG) is modulated by both anatomical and external spatial location of a remembered tactile movement target (Buchholz, Jensen, & Medendorp, 2011, 2013). In sum, both ERP and MEG studies indicate that the initial anatomical information and the remapped external spatial location of a tactile event are concurrently encoded and, presumably, subsequently integrated (cf. Badde, Heed, et al., 2015; Heed, Buchholz, et al., 2015).

One may wonder which brain regions are involved in the remapping and integration processes for tactile processing. Although there may not be one single cortical region that codes these processes, but rather a broadly distributed network, the intraparietal sulcus within the posterior parietal cortex has frequently been associated with the integration of spatial information. In the next section, I will briefly highlight its important role in tactile spatial processing.

2.2 Posterior-parietal cortex and tactile spatial encoding

The intraparietal sulcus (IPS) in the posterior parietal cortex (PPC) is thought to play a critical role in the integration of information from anatomical and external reference frames. In primates, this region has been associated with the coding of supramodal spatial maps (Y. E. Cohen & Andersen, 2002; Graziano & Cooke, 2006; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). When activity in the human IPS is disturbed by transcranial magnet stimulation (TMS), tactile localization is impaired in external space, but not in anatomical space,

suggesting a disruption of reference frame integration (Azañón, Longo, Soto-Faraco, & Haggard, 2010). Similarly, IPS has been associated with external reference frame encoding using TMS in visual-tactile (Bolognini & Maravita, 2007) and in audio-tactile interactions (Renzi et al., 2013). Further, a functional magnetic resonance imaging (fMRI) study related activity in right IPS to the position of the tactually stimulated right hand in external space (Lloyd, Shore, Spence, & Calvert, 2003). Hence, evidence from multiple neuroimaging techniques have provided compelling evidence for the involvement of IPS in the integration of spatial tactile information.

Recently, it was demonstrated that stimulating IPS with a short train of 10 Hz TMS pulses preceding tactile stimulation enhanced vibrotactile pattern discrimination at the hand ipsilateral in external space, independent of whether hands were held in an uncrossed or crossed posture (Ruzzoli & Soto-Faraco, 2014). Stimulating IPS with a train of 10 Hz TMS pulses entrains oscillatory brain activity (Thut et al., 2011). Oscillatory brain activity, thus, appears to play a critical role in the integration of spatial information for touch. In the next sections (2.3.1–2.3.3), I will detail how oscillatory brain activity is involved in the processing of spatial information.

2.3 Oscillatory brain activity

The brain must exchange information across different brain regions to transform and integrate sensory information from multiple modalities. One possibility of how the brain communicates across regions is via oscillatory brain activity (Engel, Gerloff, Hilgetag, & Nolte, 2013; Fries, 2005, 2015). Oscillatory brain activity is observed when groups of neurons synchronize their firing repetitively, possibly, because they are transiently involved in the same computation. Dynamic changes of the synchronized activity pattern can flexibly alter the brain's communication at multiple spatial and temporal scales (Engel et al., 2013; Fries, 2005, 2015). Flexible changes of the brain's communication allow for adaptation to specific task requirements. Supportive of this idea is that rhythmic oscillatory brain activity has been shown to be associated with a number of cognitive functions, including sensorimotor functions, multisensory integration, attentional selection, and working memory (Engel & Fries, 2010; Foxe & Snyder, 2011; Lisman & Jensen, 2013; Senkowski & Engel, 2012; Siegel, Donner, & Engel, 2012; Singer, 1999). However little is known about coordinated neuronal activity at

the population level and its contribution to encode information in tactile spatial reference frames. One aim of the present thesis is to investigate the involvement of alpha- and beta-band frequencies in the encoding of spatial reference frames. The possible functions of these frequency bands and their involvement in the coding of spatial information will be described in the following.

2.3.1 Alpha-band oscillations

In his pioneering work Hans Berger (1929) described patients who had lost parts of the skull after surgery. This allowed him to record the relatively weak electrical activity of the brain: the human electroencephalogram (EEG). He described the EEG as an ongoing, constantly fluctuating curve, in which one can differentiate between first order waves with an average length of 90 ms and second order waves with an average length of 35 ms (P. D. H. Berger, 1929, p. 567). The most prominent rhythm he reported is known as the alpha rhythm, which varies in its peak frequency between individuals in the range of 7–14 Hz (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014). Because the amplitude of posterior alpha-band activity increases with closed eyes, it has been thought to reflect cortical idling for a long time (Adrian & Matthews, 1934; Pfurtscheller, Stancák Jr., & Neuper, 1996). In recent years, however, alpha-band activity has been linked to active cognitive processing during a number of tasks, for instance, during working memory and spatial attention tasks (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). During covert spatial attentional deployment, alpha-band activity has been reported to be suppressed over task-relevant sensory cortices in the hemisphere contralateral to the attended location and to be enhanced over ipsilateral task-irrelevant areas. In the visual and auditory modality, covert attentional orienting to one of the hemifields is accompanied by lateralized alpha-band activity over occipital and parietal areas with a relative suppression of contralateral compared to ipsilateral alpha-band activity (Banerjee, Snyder, Molholm, & Foxe, 2011; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). Similarly, tactile attentional orienting to one hand is accompanied by lateralized alpha-band activity over central and parietal areas with a relative contralateral suppression compared to ipsilateral activity (Anderson & Ding, 2011; Bauer, Kennett, & Driver, 2012;

Haegens, Händel, & Jensen, 2011; Haegens, Luther, & Jensen, 2012; van Ede, de Lange, Jensen, & Maris, 2011). In addition, alpha-band suppression predicts subsequent sensory performance in the visual and tactile modality (Haegens et al., 2011; Thut et al., 2006; van Ede, Köster, & Maris, 2012) and may play a causal role in spatial attentional biasing, as evident when entraining IPS activity through 10 Hz TMS pulses and when subsequent visual detection performance (Romei, Gross, & Thut, 2010) and tactile discrimination performance was assessed (Ruzzoli & Soto-Faraco, 2014). Because alpha-mediated spatial attentional biasing is observed across visual, auditory, tactile modalities, it has been suggested to reflect a general supramodal mechanism (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007). Specifically, enhanced alpha-band activity is thought to reflect active inhibition, which reduces processing capabilities of a given area, alpha-band suppression is thought to reflect a gating mechanism that determines the readiness of neural populations to process sensory afferents.

2.3.2 Beta-band oscillations

In addition to alpha-band activity, beta-band oscillations (approx. 14-30 Hz) are involved in sensory and cognitive processing (e.g., Engel & Fries, 2010; Fries, 2015). In the somatosensory system, beta-band oscillations are suppressed in contralateral compared to ipsilateral cortex during tactile stimulus processing (Bauer, Oostenveld, Peeters, & Fries, 2006; Cheyne et al., 2003) and during the anticipation of tactile stimulation (Bauer et al., 2012; Jones et al., 2010; van Ede et al., 2011; van Ede, de Lange, & Maris, 2013; van Ede, Jensen, & Maris, 2010). Further, beta-band suppression in somatosensory areas has been correlated with tactile detection rates (Jones et al., 2010; van Ede, Köster, et al., 2012). Thus, contralateral alpha- and beta-band suppression appear to behave in a similar fashion and may, therefore, reflect a similar somatosensory gating mechanism (Jones et al., 2010; van Ede, Köster, et al., 2012). Despite their similarities, both frequency bands show also very different behavior under certain conditions. First, GABAergic pharmacological interventions selectively affect beta-band activity, but not alpha-band activity (Jensen et al., 2005). Second, alpha- and beta-band oscillations appear to propagate differently through the somato-motor network (van Ede & Maris, 2013). For example, electrical muscular activity of the forearm flexors and activity in contralateral sensorimotor regions oscillate coherently in the beta-band, but not in the alpha-band range,

in expectation of tactile stimulation, independent of motor commands (van Ede & Maris, 2013). In sum, activity in the alpha- and beta-band is similarly suppressed in anticipation of tactile stimulation as well as following tactile stimulation, but appears, nevertheless, to reflect distinct cortical mechanisms.

2.3.3 Oscillatory activity and spatial reference frames

How does oscillatory brain activity mirror spatial reference frames? With regards of the visual modality, it was recently investigated how the updating of visual space following a saccade is reflected in oscillatory brain activity (Van Der Werf, Buchholz, Jensen, & Medendorp, 2013).

In this task, participants fixated a cross at the beginning of each trial and a visual stimulus was shortly flashed in the left or right hemifield. Thereafter the fixation cross jumped to a new location, which required a first saccade of the participants and, thus, an updating of visual space. After a delay, participants executed a saccade to the remembered location of the visual flash. The authors examined how oscillatory activity related to the stimulus representation would reorganize to encode the remembered stimulus position relative to the updated eye fixation direction. Posterior parietal alpha-band lateralization was found to be related to the updating of visual space relative to an external eye-centered reference frame following the first saccade (Van Der Werf et al., 2013). Corroborating this finding, a recent study related posterior parietal alpha-band activity to the updating of visual space relative to an eye-centered reference frame following passive whole body motion (Gutteling, Selen, & Medendorp, 2015). Participants had to remember the spatial location of a visual target stimulus that was presented shortly before their whole body was passively shifted to one side of the room by moving the chair they sat on, requiring an updating of visual space (Gutteling et al., 2015). After the passive whole body motion, participants compared the remembered target location with the location of a visual probe. Critically, in some conditions the passive whole body motion changed the relation of the target stimulus relative to the eyes' fixation in such a way that the location of the remembered target location changed from one hemifield to the other. In these conditions, posterior parietal alpha-band activity was suppressed contralateral to the visual target stimulus location directly following stimulus presentation; in contrast, following the whole body motion activity was suppressed in the opposite hemisphere as before passive

whole body motion (Gutteling et al., 2015). Moreover, visual stimuli were presented at different spatial depths relative to a world-fixed fixation point. This manipulation allowed dissociating activity related to an eye-centered and activity related to a body-centered reference frame. For instance, the remembered location of a *distant* target stimulus, that is, farther away than the fixation point, was shifted to the left relative to the fixation point during a leftward movement.

In contrast, the remembered location of a *nearby* target stimulus, that is, between the fixation point and the participant, was shifted to the right during a leftward movement. In contrast, remembered target locations were always shifted to the right relative to the body during leftward body motion. With the manipulation of the spatial depth of the target stimuli, the authors were able to relate the modulations in posterior-parietal alpha-band activity to an eye-centered reference frame rather than an encoding relative to a body-centered reference frame (Gutteling et al., 2015). Thus, posterior parietal alpha-band activity appears to be involved in the updating of visual space relative to an external eye-centered reference frame following both saccadic eye movements and passive whole body motion.

Regarding tactile processing, Buchholz and colleagues (Buchholz et al., 2011, 2013) investigated anatomical and external spatial reference frames in the context of planning a movement to a remembered tactile targets. In their study, participants fixated the ring finger of one hand and received a tactile target stimulus at the same hand's index or little finger. After a delay, they were asked to execute either an eye (Buchholz et al., 2011) or a hand movement (Buchholz et al., 2013) to the remembered target location. During the movement planning phase, posterior-parietal alpha-band oscillations were suppressed in the contralateral compared to the ipsilateral hemisphere relative to the tactile stimulus location in an eye-centered reference frame, that is, left versus right visual hemifields (Buchholz et al., 2011, 2013). In contrast, central alpha-, and central and posterior beta-band activity were suppressed in the contralateral compared to the ipsilateral hemisphere relative to the anatomical stimulus location, that is, left versus right hand, and unaffected by the external spatial location of the target (Buchholz et al., 2011, 2013). Thus, posterior-parietal oscillatory alpha-band activity appears to be involved in the encoding of an eye-centered external reference frame for vision and touch. Yet, it is unclear whether

alpha-band activity similarly encodes external spatial information during tactile attentional processing.

Most studies investigating the role of oscillatory brain activity in tactile attentional processing did not vary direction of the eye fixation or hand posture (Anderson & Ding, 2011; Bauer et al., 2012, 2006, Haegens et al., 2011, 2012; Jones et al., 2010; van Ede et al., 2011, 2013, 2010; van Ede, Köster, et al., 2012; van Ede & Maris, 2013). Thus, it has not been possible to dissociate anatomical and external spatial reference frames in these studies. Crossing the hands over the midline allows misaligning anatomical and external spatial reference frames (Fig. 2.1B). In the present thesis, this manipulation was used to investigate the role of alpha- and beta-band oscillations in the encoding of spatial reference frames during the orienting of spatial attention in expectation of tactile stimulation (Chapter 3) and during attention-related tactile stimulus processing (Chapter 4).

2.4 Development of multisensory processing

Multisensory processing is immature at birth and critically depends on sensory experience (Knudsen & Knudsen, 1990; Stein, 2012a). For instance, the prevalence of multisensory neurons in the cat's SC increases across the life-span, presumably leading to an increase in the capacity to integrate multisensory inputs (Wallace & Stein, 1997, 2001). Strikingly, manipulating sensory experience during early life modulates responses of the cat's SC neurons: Visual deprivation, that is, dark-rearing of the animal, impairs interactions between visual and non-visual modalities (Wallace, Perrault, Hairston, & Stein, 2004). Moreover, response properties of SC neurons are dramatically altered when audio-visual co-occurrence properties in the animal's environment are modulated during ontogeny: When audio-visual stimuli are linked in time, but separated in space, some SC neurons show enhanced responses for spatially disparate audio-visual stimuli rather than for spatially coincident audio-visual stimuli, that is, a reversal of the *spatial principle of multisensory integration* (Wallace & Stein, 2007). Thus, multisensory integration does not automatically develop as a process of maturation, but depends on early sensory experiences.

In humans, it is thought that some multisensory functions emerge early in the development and that these functions improve during infancy as children grow and are exposed to sensory experiences (Lewkowicz, 2012; Lewkowicz & Röder, 2012). For instance, the ability to integrate

visual and auditory information for spatial eye and head orientation develops during the first year of life (Neil, Chee-Ruiter, Scheier, Lewkowicz, & Shimojo, 2006), whereas statistically optimal multisensory integration of visuo-haptic information appears to develop with a protracted trajectory and is not observed before the age of 8 years (Burr & Gori, 2012; Gori, Del Viva, Sandini, & Burr, 2008). In addition, the size of the temporal *multisensory binding window* (cf. Section 2.1), that is, the range, in which a multisensory interaction is likely to be observed, for audio-visual stimuli also shows an age-dependent decrease over a protracted time course that extends even into adolescence (Hillock-Dunn & Wallace, 2012). For ethical reasons long term sensory deprivation studies or manipulating environmental statistic properties in humans is not feasible. However, individuals who are deprived of one sensory modality for a period of time due to an illness or an accident offer a unique model to investigate how altered sensory input modulates multisensory processing (Pavani & Röder, 2012). For instance, congenital and profound deafness can modulate somatosensory-visual interactions: Deaf but not normally hearing individuals are reportedly susceptible to a visual double flash illusion that is induced by two subsequently presented tactile stimuli at the face (Karns, Dow, & Neville, 2012). Moreover, individuals deprived of pattern vision for the first months of life as a result of congenital binocular cataracts exhibit impaired audio-visual interactions, as evident in an attenuated interference of an auditory distractor during a temporal visual identification task (Putzar, Goerendt, Lange, Rösler, & Röder, 2007). Thus, postnatal sensory experience shapes multisensory functions also in humans.

Congenitally blind individuals provide another model to investigate the influence of sensory deprivation on multisensory processing (Hötting & Röder, 2009; Occelli, Spence, & Zampini, 2013).

Indeed, individuals who are born blind due to peripheral reasons show a number of altered multisensory interactions in the preserved modalities, that is, audio-tactile interactions (e.g., Collignon, Charbonneau, Lassonde, & Lepore, 2009; Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006; Hötting & Röder, 2004; Hötting, Rösler, & Röder, 2004; Occelli, Bruns, Zampini, & Röder, 2012; Occelli, Spence, & Zampini, 2008). Such altered multisensory interactions are related to both spatial and temporal features (for a review see Occelli et al., 2013). As the present thesis is focused on spatial aspects of multisensory

integration via measures of tactile localization, I will highlight some examples that addressed the influence of developmental vision on spatial multisensory interactions. For instance, congenitally blind, but not sighted, individuals benefit from redundant spatial information in audio-tactile TOJ, that is, when stimuli are presented to different compared to the same spatial location (Occelli et al., 2008). Moreover, congenitally and early blind compared to sighted individuals show a reduced audio-tactile integration with crossed hands: when localizing auditory, tactile, and bimodal events early blind individuals show faster reaction times for bimodal than for unimodal stimuli (Collignon et al., 2009). Yet, this enhancement is only faster than what is predicted by the combined unisensory conditions (i.e., a violation of the race model) with uncrossed hands, but not with crossed hands. In contrast, in sighted individuals this enhancement is faster than the prediction independent of the hand posture (Collignon et al., 2009). Similarly, hand crossing has been reported to impair audio-tactile integration in congenitally blind individuals in the context of the modified audio-tactile ventriloquist illusion (Occelli et al., 2012): spatially discrepant tactile distractors bias auditory localization towards the location of the tactile stimulus with uncrossed, but not with crossed hands. In contrast, in sighted this bias is evident with uncrossed and crossed hands (Bruns & Röder, 2010; Occelli et al., 2012). Taken together, visual deprivation from birth on critically modulates spatial multisensory interactions. As discussed, multisensory spatial information contributes to tactile localization. Thus, it is likely that developmental vision alters tactile localization. Further evidence for the impact of developmental vision on tactile localization is provided in the next section.

2.5 Developmental vision and tactile localization

Regarding tactile localization, developmental vision critically influences how spatial features of touch are processed (Collignon, Charbonneau, Lassonde, & Lepore, 2009; Eardley & van Velzen, 2011; Heed, Möller, & Röder, 2015; Röder et al., 2008; Röder, Rösler, & Spence, 2004). In contrast to sighted individuals, congenitally blind individuals do not integrate external and anatomical spatial information by default when localizing tactile stimuli (Collignon et al., 2009; Röder et al., 2008, 2004). This is evident when misaligning spatial reference frames by hand crossing (see Fig. 2.1B), which reduces tactile localization performance in sighted, but not in congenitally blind individuals (Collignon et al.,

2009; Röder et al., 2004). In addition, attention-related effects on somatosensory ERPs have been reported to be reduced by hand crossing in sighted, but not in congenitally blind individuals (Röder et al., 2008). These findings suggest that the default encoding of external spatial features of touch develops under the influence of the visual system during ontogeny. In accord with this notion is that children younger than five and a half years do not integrate external spatial information in touch by default, whereas children older than five and a half years do (Pagel, Heed, & Röder, 2009). Furthermore, late blind individuals, similarly to sighted but contrary to congenitally blind individuals, appear to integrate external spatial information by default for proprioceptive reach targets (Reuschel, Rösler, Henriques, & Fiehler, 2012) and for tactile localization (Röder et al., 2004), suggesting that especially early visual experiences play a role in how space is encoded. However, the underlying neural mechanisms of the differential encoding of spatial tactile features between sighted and congenitally blind are unknown.

Differences in the amplitudes of oscillatory activity between normally sighted and visually deprived individuals have been reported before: The amplitude of the alpha-band is markedly reduced in congenitally blind individuals (R. J. Berger, Olley, & Oswald, 1962; Birbaumer, 1971; Kriegseis, Hennighausen, Rösler, & Röder, 2006; Novikova, 1973) and in individuals who had suffered from bilateral congenital dense cataracts and regained vision later in life (Bottari et al., 2016). In addition, the frequency that dominates the occipital EEG signal increases with age (Lindsley, 1939).

In one-month olds the occipital EEG is dominated by a 4 Hz rhythm, whereas in older children the dominating frequency is increased until an average frequency around 10 Hz is reached at approximately twelve years of age (Lindsley, 1939). Together, these findings suggest that the access to visual information during infancy is critical for the mechanisms that generate oscillatory alpha-band activity. In normally sighted individuals, alpha-band activity has been associated with an eye-centered external spatial coding in the updating of visual space and in the context of movement planning to remembered tactile targets (section 2.3.3; Buchholz et al., 2011, 2013; Gutteling et al., 2015; Van Der Werf et al., 2013). Alpha-band activity may, thus, play a role in the coding of eye-centered external spatial information during the deployment of tactile attention and during tactile processing in sighted

individuals. Differences in oscillatory alpha-band activity between sighted and congenitally blind individuals may relate to their differential integration of anatomical and external spatial information for touch. In the present thesis, I, therefore, investigate how the orienting of spatial tactile attention (Chapter 3) and the processing of spatial features of tactile stimuli (Chapter 4) modulates oscillatory activity differently in the presence and in the absence of developmental vision.

2.6 Flexible integration of spatial information

Multisensory integration has been shown to depend on the current task demands, as evident in bottom-up modulations when the sensory signal of one modality is degraded (Ernst & Banks, 2002) and in top-down modulations when attentional resources are restrained in the context of a dual-task paradigm (Alsius, Navarra, Campbell, & Soto-Faraco, 2005; Alsius, Navarra, & Soto-Faraco, 2007). As mentioned above, in tactile localization the relative weight of external and anatomical spatial information for integration appears to depend on specific task demands, as demonstrated in studies employing tactile TOJs (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015). Another possibility to investigate tactile localization is testing how task-irrelevant distractor stimuli interfere with tactile localization (Spence, Pavani, Maravita, & Holmes, 2004). Tactile localization is reportedly faster and more accurate when a visual distractor is simultaneously presented at a congruent as compared to an incongruent elevation (Spence, Pavani, & Driver, 2000). Similarly, tactile distractors have been reported to interfere with the localization of tactile target stimuli (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Soto-Faraco, Ronald, & Spence, 2004). In a study by Soto-Faraco and colleagues (2004), participants held two foam cubes between each hand's thumb and index finger with palms facing down. Participants had to indicate the elevation, that is, "up" or "down" in space, of a tactile target stimulus as fast and accurately as possible by means of a foot pedal. The target stimulus was randomly delivered to the index finger or the thumb of one hand. A tactile distractor stimulus was presented simultaneously either at a congruent or incongruent location of the other hand and had to be ignored. Critically, hand posture was varied to probe spatial reference frames, with either both palms facing in the same direction, that is, up or down, or in different directions, that is, with one palm facing up and the other down. Importantly, congruency could be defined in two ways: relative to

anatomical space, that is target–distractor pairs were presented to congruent skin locations (e.g. at both index fingers), or relative to external space, that is target–distractor pairs were presented at congruent elevations (e.g. both “up” in space). If both hands were placed in the same posture, for example, both palms were facing down, anatomical and external congruencies corresponded. When hands were placed in different postures, anatomical and external congruency opposed each other and anatomical congruent locations were incongruent in external space and vice versa. The manipulation of hand posture, thus, offers the possibility to study the weighting of anatomical and external spatial information. Participants judged the elevation of tactile target stimuli faster and more accurately following target–distractor pairs presented to congruent compared to incongruent elevations, independent of hand posture, suggesting that congruency was encoded relative to an external spatial reference frame (Gallace et al., 2008; Soto-Faraco et al., 2004). Yet, congruency effects were encoded relative to an anatomical reference frame when participants were asked to verbally indicate the anatomical location of the tactile target stimulus, that is, index finger vs. thumb, with faster and more accurate responses following anatomically congruent than incongruent target–distractor pairs (Gallace et al., 2008). Therefore the evidence suggest, that anatomical and external spatial information is weighted for the coding of congruency effects between tactile targets and tactile distractors and modifiable by task instruction and response modalities. In line with such flexible weighting of spatial information, a number of factors have been shown to modulate the integration of anatomical and external spatial information in sighted individuals. For instance, external spatial information has been reported to be weighted more strongly when the context of a secondary task emphasizes external rather than anatomical space (Badde, Röder, et al., 2015), when non-informative vision is available (Newport, Rabb, & Jackson, 2002), in the context of movements (Gherri & Forster, 2012a, 2012b; Heed, Möller, et al., 2015; Hermosillo, Ritterband-Rosenbaum, & van Donkelaar, 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett, Carnevale, & Harris, 2012), and in the context of frequent posture changes (Azañón, Stenner, Cardini, & Haggard, 2015).

In contrast, not much is known about the factors that modulate the integration of anatomical and external spatial information in congenitally blind individuals. The above discussed studies suggest that

congenitally blind individuals rely predominantly on anatomical information when localizing touch (Collignon et al., 2009; Röder et al., 2008, 2004). Recent evidence, however, suggests that congenitally blind individuals do integrate external spatial information under certain task demands. For instance, congenitally blind individuals integrated external and anatomical spatial information for tactile localization while making bimanual movements (Heed, Möller, et al., 2015). In addition to tactile localization tasks, another recent study indicated, too, that congenitally blind individuals do integrate external spatial information: The symmetry of bimanual finger movements appeared to be encoded relative to external space rather than according to anatomical parameters such as the involved muscles (Heed & Röder, 2014). Moreover, the mental representation of time is encoded relative to external space both in sighted and in early blind individuals (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015). This latter finding was hypothesized to be related to Braille reading experience in blind individuals (Bottini et al., 2015). Such a relation, in turn, would link the coding of external spatial information again to manual movements. Thus, the motor system may be involved in the coding of external spatial information in both sighted and congenitally blind individuals.

Given that task instructions can emphasize the weighting of external spatial information for tactile localization in sighted individuals (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015; Gallace et al., 2008), they may have a similar impact in congenitally blind individuals. In the auditory modality, when auditory events are linked to external space, an integration of external spatial information has been observed in congenitally blind individuals (Röder, Kusmirek, Spence, & Schicke, 2007). In the tactile modality, only indirect evidence is currently available that suggests an influence of task instruction on tactile localization in congenitally blind individuals.

Two very similar studies investigated attention-related effects on somatosensory ERPs with uncrossed and crossed hands in early and congenitally blind adults (Eardley & van Velzen, 2011; Röder et al., 2008). Both studies cued participants to attend to one of their hands to detect rare tactile target stimuli on that hand. Surprisingly, the two studies observed a different result pattern: One study reported a significant effect of hand posture on attention-related somatosensory ERPs to non-target stimuli (Eardley & van Velzen, 2011), whereas the other study did not (Röder et al., 2008). Results of the first study, thus,

suggested an integration of external spatial information in tactile spatial processing in early blind participants (Eardley & van Velzen, 2011), whereas the second study concluded that congenitally blind humans do not, by default, integrate external spatial information of touch (Röder et al., 2008). Critically, the two studies differed in how participants were instructed about the task-relevant location. In the first study, cueing indicated the task-relevant side relative to external space in each trial (Eardley & van Velzen, 2011). In the second study, in contrast, cueing indicated the task-relevant hand, independent of hand location in external space (Röder et al., 2008). Thus, task instructions may modulate how anatomical and external information is integrated in both sighted and congenitally blind individuals.

In the present thesis, I study how task requirements affect the weighting of anatomical and external spatial information in sighted and congenitally blind individuals in a tactile congruency task (Chapter 5; cf. Gallace et al., 2008; Soto-Faraco et al., 2004). To this end, two factors were manipulated. First, participants received two different instructions: Participants were instructed to localize tactile target stimuli presented at their hands either relative to the anatomical skin location or relative to the location in external space. Second, hand posture was either fixed throughout an entire block or it varied in a trial-by-trial fashion to test whether the dynamic context of frequent posture changes emphasized the weighting of external spatial information similarly in sighted and congenitally blind individuals.

2.7 Movement planning and tactile processing

As reviewed above, tactile localization involves the integration of sensory information coming from different senses. Yet, sensory information is not only integrated for the sake of integration or tactile localization itself, but to enable us to interact with the environment via eye and limb movements. In the primate brain, multisensory information about space, which is thought to be integrated in the posterior parietal cortex (Y. E. Cohen & Andersen, 2002; Graziano & Cooke, 2006), appears to be transferred from parietal to motor regions via direct and effector specific circuitries (i.e., specific for eye, hand, and, possibly, foot movements) (Matelli & Luppino, 2001). In the human visual system, saccade planning and covert spatial attention have been proposed to share the same underlying neural mechanisms, as formulated in the so-called premotor theory of attention (Rizzolatti,

Riggio, Dascola, & Umiltà, 1987). In line with this idea, both saccades and covert spatial attention activate highly overlapping brain areas as revealed by fMRI research (Corbetta, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000). One of the claims of the premotor theory of attention is that movement planning enhances sensory perception at the location of the movement goal prior to movement onset (Rizzolatti, Riggio, & Sheliga, 1994). When planning a saccade, behavioral discrimination performance is indeed enhanced at the saccade goal compared to a control location for visual (Baldauf & Deubel, 2008b; Collins & Doré-Mazars, 2006; Deubel & Schneider, 1996; Doré-Mazars, Pouget, & Beauvillain, 2004; Jonikaitis, Pöpper, & Deubel, 2011; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), auditory (Rorden & Driver, 1999), and tactile stimuli (Juravle & Deubel, 2009; Rorden, Greene, Sasine, & Baylis, 2002). In addition, stimuli presented at the goal of a planned saccade compared to stimuli presented at a control location elicit enhanced visual, somatosensory, and auditory ERP amplitudes in the same time ranges, during which an enhancement by covert spatial attention had been observed (Collins, Heed, & Röder, 2010; Eimer, Van Velzen, Gherri, & Press, 2006; Gherri, Driver, & Eimer, 2008; Gherri & Eimer, 2008). For instance, in the tactile modality somatosensory ERPs are enhanced between 130 and 170 ms poststimulus by covert spatial attention and by planning a finger lift (Gherri & Eimer, 2008).

The saccadic system and covert spatial attention may, thus, indeed share the same neural mechanisms. The premotor theory of attention was soon extended to manual movements. Similar to saccade planning, the planning of manual pointing, reaching, and grasping movements reportedly enhances visual discrimination performance at the movement goal compared to non-goal control locations (Baldauf, Wolf, & Deubel, 2006; Collins, Schicke, & Röder, 2008; Deubel & Schneider, 2004; Deubel, Schneider, & Paprotta, 1998; Rolfs, Lawrence, & Carrasco, 2013; Schiegg, Deubel, & Schneider, 2003). Similarly, visual ERPs are enhanced in the time range of the N1 when elicited by visual probe stimuli at manual movement goals compared to control locations (Baldauf & Deubel, 2008a). Little is known about how goal-directed limb movements with effectors affect tactile processing. Planning to lift a finger or to press a button reportedly enhances tactile discrimination performance at the effector finger (Juravle & Deubel, 2009; van Ede, van Doren, Damhuis, de Lange, & Maris, 2015). Yet, these movements are not goal-directed and they do not allow differentiating between

effector and movement goal. The effector and movement goal have been dissociated in an ERP study that asked participants to reach with one hand towards the other (Forster & Eimer, 2007). Specifically, participants were asked to plan a movement and to ignore tactile stimuli presented to either hand during movement planning. Somatosensory ERPs were enhanced in the range of the N140 when elicited by tactile stimuli presented at the effector hand compared to tactile stimuli at the movement goal. The authors concluded that movement planning shifted tactile attention to the effector, and not to the movement goal (Forster & Eimer, 2007). This conclusion was indirectly drawn based on a comparison with previous studies that reported a modulation by covert tactile attention in the same time range (Eimer et al., 2003; Forster & Eimer, 2007; Michie, Bearpark, Crawford, & Glue, 1987). However, in the study by Forster and Eimer (2007) tactile stimuli were presented to the hands only, which served in all trials either as effector or as a movement goal, but never at a movement-irrelevant control location. Thus, stimulus processing at the movement goal may still be enhanced in comparison to a movement-irrelevant control location.

Moreover, little is known about the involvement of spatial reference frames in tactile attention shifts related to goal-directed movement planning of a limb. Saccade planning and planning of a non-goal-directed finger lift appear to shift tactile attention according to an external spatial reference frame: Saccadic planning effects on tactile discrimination performance (Rorden et al., 2002) and effects of manual non-goal-directed and saccadic movement planning on somatosensory ERPs (Gherri & Forster, 2012a, 2012b) have been reported to not significantly differ between uncrossed and crossed hands. In the present thesis, in a set of three experiments I investigate how goal-directed movements with the head and with the hands modulated tactile processing at the goal and at the effector of a movement, and how anatomical and external spatial reference frames were involved in such modulations (Chapter 6).

2.8 Thesis at a glance

In the present thesis, I address the question of how the brain selects and integrates information from the myriad of sensory signals available at every moment to achieve a coherent percept of the world. The study of tactile processing is an approach that helps answering this question.

Here, I investigate how the following factors influence the processing of touch: First, the studies examine how anatomical skin-based and posture-related external spatial information contribute to tactile processing (all studies; Chapters 3–6). Second, a series of studies explores the influence of developmental vision on spatial processing of touch (Chapters 3–5). Third, the thesis investigates the underlying neural processes using measures of oscillatory brain activity, of spatial coding for touch in the presence and absence of developmental vision (Chapters 3 & 4). Fourth, the thesis addresses the question of how task instructions and frequency of posture change influence tactile localization (Chapter 5). Fifth, the present work further details how goal-directed movement planning modulates tactile processing at the movement goal and at the effector (Chapter 6). Finally, I discuss the findings in the general context of their implications and I will end with an outlook for future directions in the field of spatial encoding of touch (Chapter 7).

Chapter 3:

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

Adapted from:

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3.1 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 & 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 central and posterior beta-band activity appear to be modulated by anatomical coordinates only 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.

3.2 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.

3.2.1 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 (2000) and the ethical requirements of the University of Marburg, where the data for this study were acquired.

3.2.2 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 (Fig. 3.1). 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, Hink, Schwent, & Picton, 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. 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.

3.2.3 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 Ω . The right earlobe served as reference during recording.

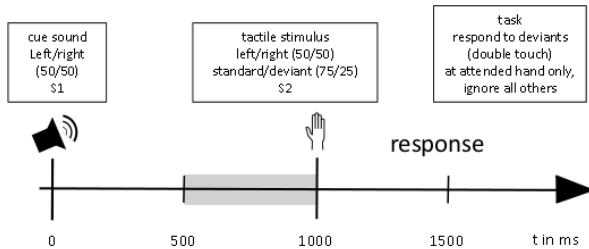


Figure 3.1. Schematic trial structure. Each trial started with an auditory cue to indicate the task relevant finger during that trial ($t = 0$). After 1000 ms a tactile stimulus (standards and deviants) was presented either to the left or to the right hand. Participants had to respond to rare tactile 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 grey shaded box).

3.2.4 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 & 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).

3.2.5 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, Fries, Maris, & Schoffelen, 2011) in the Matlab environment (Mathworks, Natick, MA). Data was re-referenced to an average reference (Schneider, Debener, Oostenveld, & Engel, 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.

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. S3.1 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. 3.4 & 3.6): a frontal cluster (electrode positions approximately corresponding to F3/4, FC1/2, and FC3/4 of the 10–10 system (Oostenveld & 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, Hohlefeld, Curio, & Nikulin, 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; Buchholz, Jensen, & Medendorp, 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 (Fig. 3.2A-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 controls (Birbaumer, 1971; Kriegseis et al., 2006; Noebels, Roth, & Kopell, 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 (Fig. 3.4 & 3.6; 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).

In order to explore task-related changes of oscillatory power, we \log_{10} -transformed power related to directing attention to the 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, de Lange, & Maris, 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 & Feldt, 1976); we report the original degrees of freedom with corrected p -values.

3.2.6 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 & Oostenveld, 2007).

In the sighted group, a prior analysis (Röder et al., 2008) had revealed a modulation of d' -scores and alpha-band lateralization 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).

3.2.7 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, Kujala, Jensen, & Salmelin, 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, van Drongelen, Yuchtman, & Suzuki, 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, Kastner, Wagner, Hawes, & Ebersole, 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 & 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 & 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 ($10 \text{ Hz} \pm 3.33 \text{ Hz}$) 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.

3.3 Results

3.3.1 Behavioral performance

Posture significantly influenced behavior in the sighted group only (Fig.3.7A; Group – Posture inter-action: $F(1, 22) = 5.87$, $p = 0.024$), 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 ($t(22) = 0.98$, $p = 0.337$).

3.3.2 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 (Fig. 3.2A-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. 3.2), 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 Fig. 3.2A,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.3.2D, 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.

3.3.3 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. 3.3 & 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 (Fig. 3.3 A, C, F & Fig. 3.4 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 (Fig. 3.4 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. 3.4 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. 3.4 A, all $F < 1$).

In contrast to the sighted group, for the blind group (Fig. 3.3 D–F, Fig. 3.4 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 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. S3.1A-I). Consistent with the results presented here, the contrast of alpha-band activity between hands (Fig. S3.1G,H) was modulated by hand posture in the sighted group (Fig. S3.1, left column), but not in the blind group (Fig. S3.1, 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.

3.3.4 Modulation of beta-band activity by tactile attention

Analysis of the beta-band (Figs. 3.5 & 3.6) 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, $F(1,22)=0.11$, $p = 0.740$; 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 S3.1R). 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.

3.3.5 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.3.7B, CBPT: $p < 0.001$) and with crossed hands (Fig. 3.7C, 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- or the beta-band.

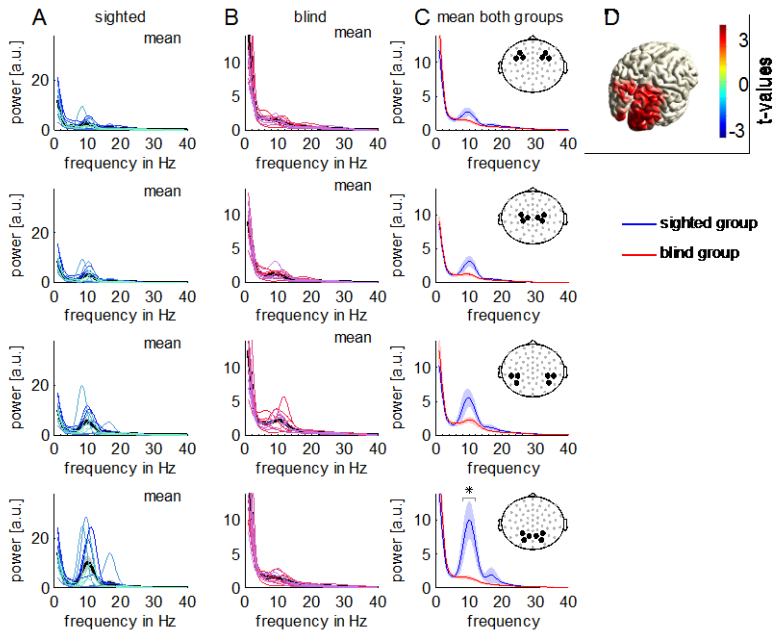


Figure 3.2. Spectral power during baseline. Activity between trials, **A**, in the sighted and, **B**, in the congenitally blind group averaged across electrodes within frontal, central, parietal, and parieto-occipital clusters (from top to bottom electrodes marked on the topography plot in **C**) and 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: $p = 0.038$).

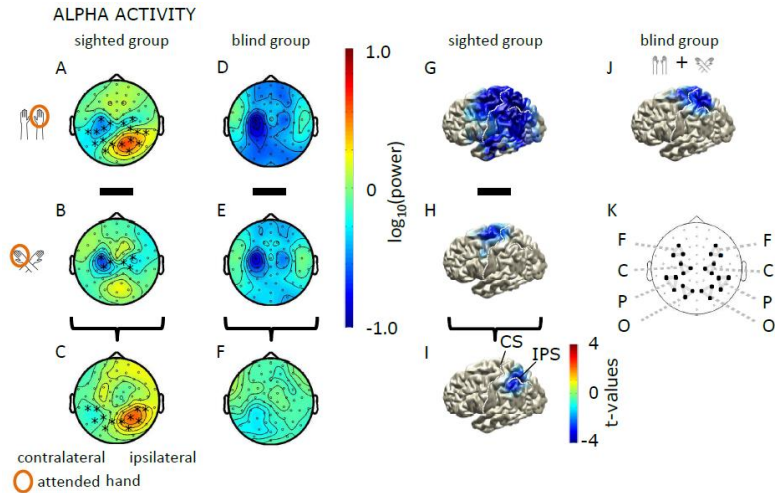


Figure 3.3. Alpha-band activity during the cue–target interval. **A–D.** Alpha-band (8–12 Hz) activity relative to baseline 500 to 1000 ms following the auditory cue, **A, D**, with uncrossed and, **B, E**, with crossed hands, **A – C**, in the sighted and, **D – F**, in the blind group. **C, F.** Topography 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 (grey triangles) used for statistical analysis at the sensor level for both alpha- and beta-band activity.

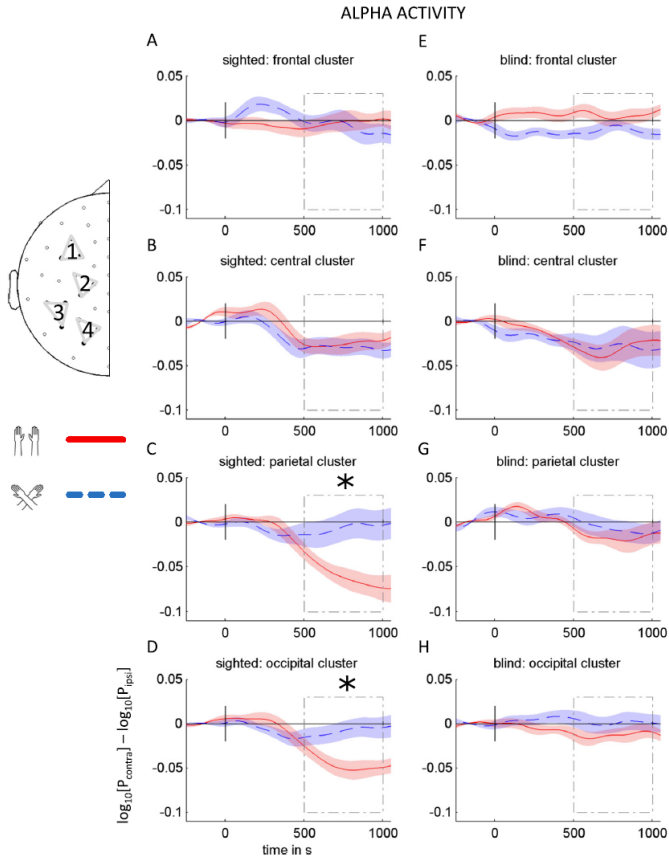
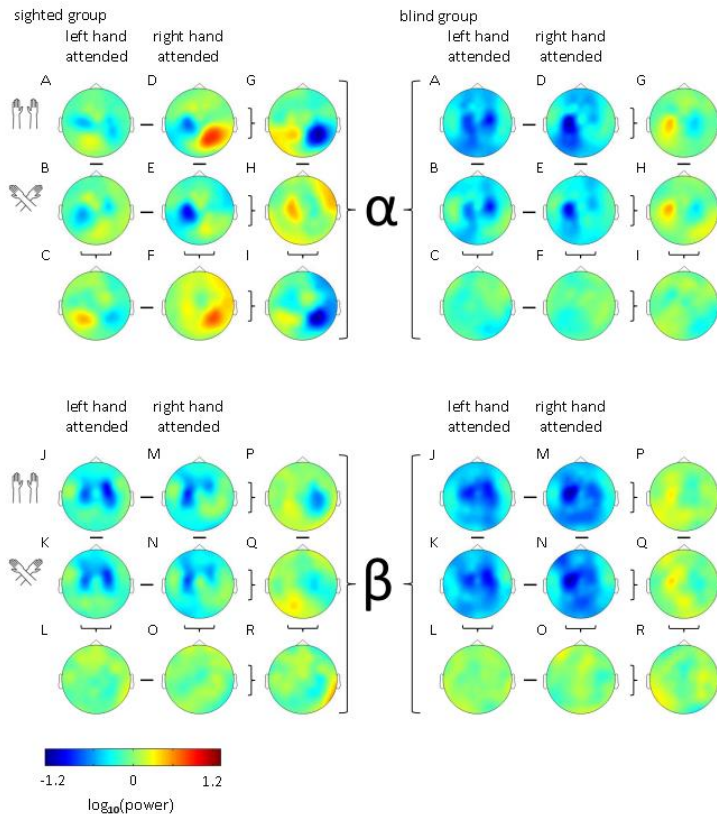


Figure 3.4. Alpha-band (8-12 Hz) lateralization over time. Analyzed electrode clusters of interest are marked with triangles on the semi-head montage, black dots mark included channels, see text for details. The difference between contralateral minus ipsilateral (relative to attended hand) log-power over time is shown for uncrossed (solid) and crossed (dashed) posture in sighted (left) and blind (right) participants. The shaded area represents the standard error of the mean. Grey 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.



Supplemental Figure S3.1. A-I, Topographies of alpha- (8-12 Hz, top) and, J-R, beta-band (16-24 Hz, bottom) 500 to 1000 ms post-cue (i.e. 500 to 0 ms pre-stimulus) in the sighted group (**left column**) and in the congenitally blind group (**right column**); A, D, J, M, with hands uncrossed; B, E, K, N, with hands crossed; A, B, J, K, left hand attended; D, E, M, N, right hand attended. G, H, P, Q. Topographies of the difference between attention to the left minus attention to the right hand, G, P, with hands uncrossed and, H, Q, crossed. C, F, L, O. Topographies of the difference uncrossed minus crossed hands, C, L, when the left and F, O, when the right hand was attended. I, R. Topographies of the interaction between posture and attended hand (i.e. the difference between left hand attended vs. right hand attended with hands uncrossed minus crossed). Note that in contrast to the main analysis data of these topographies was not remapped into contra- and ipsilateral recording sites.

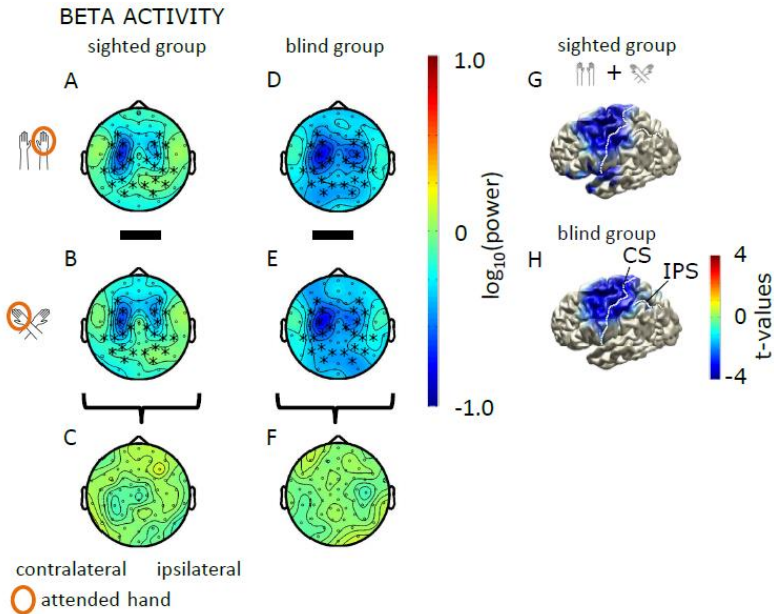


Figure 3.5. Beta-band activity during the cue–target interval. **A–D.** Beta-band (16–24 Hz) activity relative to baseline 500 to 1000 ms following the auditory cue, **A, D**, with uncrossed and, **B, E**, crossed hands, **A – C**, in the sighted and, **D – F**, in the blind group. **C, F.** Topography 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).

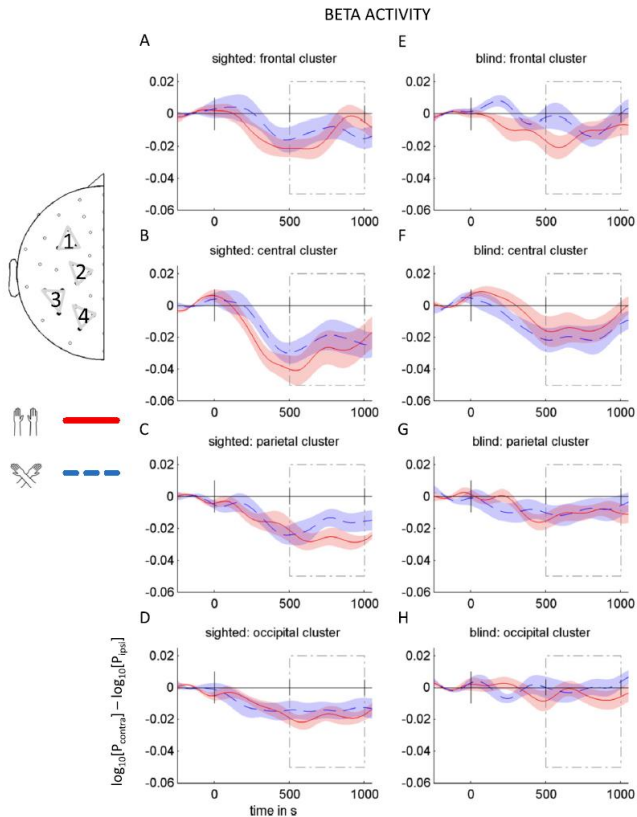


Figure 3.6. Beta-band (16-24 Hz) lateralization over time. Figure display parallels Fig. 3.4. Analyzed electrode clusters of interest are marked with triangles on the semi-head montage, black dots mark included channels, see text for details. The difference between contralateral minus ipsilateral (relative to attended hand) log-power over time is shown for uncrossed (solid) and crossed (dashed) posture in sighted (left) and blind (right) participants. The shaded area represents the standard error of the mean. Grey boxes (dash-dotted) mark the analyzed time window. The auditory cue was presented at $t = 0$.

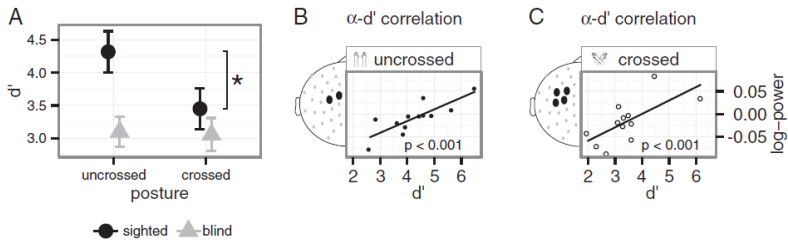


Figure 3.7. Behavioral results and behavior–physiology correlation. **A**, d' -scores in the sighted (black circles) and in the congenitally blind group (grey triangles) with uncrossed (left) and crossed hands (right). Whiskers represent the standard error of the mean. **B**, **C**. Correlation between 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. SC: sighted control group.

3.3.6 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. 3.3I; 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 (CBPT: $p = 0.049$, $p = 0.047$, $p = 0.046$, 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. 3.3G,

CBPT: $p = 0.004$, MNI: -32, -50, 68) and crossed hands (Fig. 3.3H, 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. 3.3J, 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 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.

3.3.7 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. 3.5G, CBPT: $p < 0.001$, MNI: -20, 27, 59) and in the congenitally blind group (Fig. 3.5H, CBPT: $p = 0.003$, MNI: -6, -43, 80) for central areas including M1 and S1.

3.4 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 the 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.

3.4.1 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 & 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. 3.3A). 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).

3.4.2 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. 3.7A; Röder et al., 2008). Behavioral effects of hand crossing in studies using temporal order judgment tasks (Heed & Azañón, 2014) have been associated with the integration of conflicting information from anatomical and external reference frames with crossed hands (Heed, Buchholz, 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, Deangelis, & Angelaki, 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. S3.1). 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 & 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, de Lange, 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 & 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, de Lange, et al., 2012).

3.4.3 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.3.3G) and crossed hands (Fig.3.3H), whereas lateralization in PPC appeared to be present only with uncrossed hands, but not with crossed hands (Fig.3.3I). Furthermore, the central lateralization overlapped to a great extent with the beta-band lateralization (Fig. 3.5G). 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 & 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 (Y. E. Cohen & Andersen, 2002; Graziano & 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 & 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 & 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.

3.4.4 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., 2008, 2004). 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.3.3J). 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. 3.7A). 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., 2008, 2004). Although congenitally blind individuals can make use of an external reference frame when task instructions suggest or require its use (Eardley & van Velzen, 2011; Heed & 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, van Lierop, Schrijer, & Storm van Leeuwen, 1973; Lopes da Silva, Vos, Mooibroek, & van Rotterdam, 1980; Lőrincz, Kékesi, Juhász, Crunelli, & Hughes, 2009), including the visual thalamus as well as the lower layers of the visual cortex, have been found to be atrophied in congenital blind individuals (Ptito, Schneider, Paulson, &

Kupers, 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).

3.4.5 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.

**Chapter 4:
Alpha-band oscillations reflect external
spatial coding for tactile stimuli in
sighted, but not in congenitally blind
humans**

4.1 Introduction

There is strong evidence for the involvement of oscillatory alpha-band activity in attentional processing (Foxe & Snyder, 2011). For instance, covert attentional orienting in the visual and auditory modalities is accompanied by the lateralization of alpha-band activity over occipital and parietal areas, caused by the suppression of alpha-band activity contralateral to the attended side of space, relative to ipsilateral activity (Banerjee et al., 2011; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). In the tactile modality, oscillatory alpha-band activity has been related to tactile attentional orienting to the hands (Anderson & Ding, 2011; Bauer et al., 2012; Haegens et al., 2011, 2012; Schubert et al., 2015; van Ede et al., 2011), to motor planning toward tactile targets (Buchholz et al., 2011, 2013, 2014), and to attention-related processing of tactile stimuli (Bauer, Oostenveld, Peeters, & Fries, 2006; van Ede, Szebényi, & Maris, 2014). In sighted individuals, touch is concurrently encoded in at least two spatial reference frames. The information about the touched location on the skin is encoded relative to an anatomical reference frame, and automatically combined with postural information to derive the spatial location of the tactile event in an external reference frame (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Both anatomical and external reference frames influence oscillatory activity during the orienting of attention as well as during movement planning to tactile targets. Whereas lateralization of alpha-band activity is modulated by external spatial information, beta-band lateralization is dependent on anatomical information only (Buchholz et al., 2011, 2013; Schubert et al., 2015). However, alpha- and beta-band activity play a role not only during the orienting of attention and movement planning, but also in the attentional modulation of tactile processing itself: occipital alpha- and beta-band activity are suppressed for attended versus unattended tactile stimuli (Bauer et al., 2006). Furthermore, evidence from event-related potentials (ERP) suggests that the attentional modulation of tactile processing is affected by spatial reference frames. Attention effects in somatosensory ERPs are reduced between 80 to 160 ms and between 200 and 300 ms when anatomical and external reference frames provide conflicting information, as happens when hands are crossed (Eardley & van Velzen, 2011; Eimer et al., 2003; Heed & Röder, 2010; Röder et al., 2008). Here, we hypothesize that the modulation of tactile processing by spatial attention is mediated by oscillatory alpha-band activity, and that this

modulation operates in external space. Together with prior findings (Buchholz et al., 2011, 2013; Ruzzoli & Soto-Faraco, 2014; Schubert et al., 2015) such a finding would suggest a more general role of alpha band activity to encode stimuli in external space independent of specific tasks. Another possibility to investigate the role of alpha-band activity in spatial coding is to study congenitally blind individuals. Much in contrast to sighted adults, congenitally blind individuals show a strong bias for using an anatomical reference frame (Collignon et al., 2009; Heed, Möller, et al., 2015; Röder et al., 2008, 2004). Thus, we hypothesize that alpha-band activity during stimulus processing is associated with the location of the stimulus in external space in the sighted, but not in the congenitally blind.

4.2 Materials and Methods

Analyses were performed on a dataset for which we have previously inspected alpha- and beta-band activity preceding tactile stimulation (Chapter 3; Schubert et al., 2015) and analyzed ERPs following tactile stimulation (Röder et al., 2008). The description of experimental methods is therefore confined to those details that are essential for the present analyses.

4.2.1 Participants

The dataset comprised EEG data recorded from 12 congenitally blind adults (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. Blind participants were blind from birth due to peripheral defects and were either totally blind or did not have more than diffuse light perception (Röder et al., 2008). The experiment was performed in accordance with the ethical standards laid down in the Declaration of Helsinki and the ethical requirements of the University of Marburg, where the data for this study were acquired.

4.2.2 Stimuli and Procedure

EEG was recorded from 61 equidistantly arranged electrodes at a sampling rate of 500 Hz with an analog passband filter of 0.1–100 Hz of the amplifiers (for details see Röder et al., 2008) while participants performed a tactile attention task (Fig. 3.1): Each trial started with a

centrally presented auditory cue, either a low- or a high-pitched tone, that instructed participants to attend either the right or left hand. To avoid any emphasis on an external reference frame, the cue referred to the anatomical side of the hand irrespective of hand posture, rather than to a side of space. After 1000 ms, a tactile stimulus was randomly presented to the tip of the left or right index finger. Thus, stimulation occurred either on the attended or on the unattended hand. Stimulation consisted of two metallic pins (diameter: 0.8 mm) that were briefly raised by 0.35 mm. Participants had to respond only to rare tactile deviant stimuli ($p = 0.25$) on the attended hand by depressing a foot pedal that was placed underneath the left foot in half of the experiment, and under the right in the other half. They had to ignore standard stimuli on the attended hand, and both standard and deviant stimuli at the non-attended hand. 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 stimulus duration of 200 ms. Analysis included only trials in which standard stimuli were presented, so that our analyses are free of response-related EEG artefacts. The hands were placed 40 cm apart on a table in front of the participant; positioned in an uncrossed or crossed posture (alternated blockwise, order counterbalanced across participants). The experiment consisted of 16 blocks with 96 standards and 32 deviants in each block. Each of the conditions (two hand postures, two attention cues, and two stimulus locations) comprised 192 standard stimuli.

4.2.3 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 & Swets, 1966). The d' scores as well as hits and false alarms separately were analyzed with an ANOVA for repeated measures with the between factor Group and the within factor Posture (Röder et al., 2008).

4.2.4 Analysis of EEG data

EEG analysis was performed with FieldTrip (Oostenveld et al., 2011) in the Matlab environment (Mathworks, Natick, MA). EEG signals were re-referenced to an average reference. Line noise was removed by subtracting 50 and 100 Hz components estimated by discrete Fourier

transform (van Ede et al., 2011). Data were segmented into 2500 ms epochs lasting from 500 ms before auditory cue onset (that is, 1500 ms before tactile stimulus onset) until 1000 ms post-tactile stimulus onset. Epochs were visually inspected and removed if they were contaminated by muscle or eye artifacts. Because we used the entire trial interval for trial selection, we could use identical data for our previous, pre-stimulus analysis and the current post-stimulus analysis, allowing direct comparison of result patterns in the two time intervals. 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 stimulated hand (regardless of hand posture, cf. Buchholz et al., 2013). Accordingly, data are visualized as if all stimuli were presented to the right hand, and the left (right) hemisphere denotes the anatomically contralateral (ipsilateral) hemisphere relative to stimulation.

Power of oscillatory activity was estimated for frequencies in the range of 2–40 Hz in steps of 2 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 \log_{10} -transformed and averaged for each participant and condition. Power estimates from -500 to 0 ms relative to the tactile stimulus (that is, 500 ms to 1000 ms after the auditory cue onset) served as baseline. As illustrated in Fig. 4.1, oscillatory activity was modulated by the auditory cue prior to tactile stimulation; we reported on these effects in our previous paper (Schubert et al., 2015). By using the interval directly preceding tactile stimulation as a baseline, the pre-stimulus differences were eliminated and, thus, allows for an isolated analyses of attentional effects related to stimulus processing. This choice of baseline is critical to dissociate the effects of cue-related, pre-stimulus orienting of attention from the effects of an attentional modulation of tactile stimulus processing (Bauer et al., 2006).

Analyses included the between group factor Group (sighted vs. blind) and the within group factors Attention (attended vs. unattended) and Posture (hands uncrossed vs. crossed). To explore whether attention modulated posture effects differently in blind and sighted individuals, we conducted a cluster-based permutation test (CBPT) (Maris & Oostenveld, 2007). This test controls the false alarm rate for the multiple comparisons across multiple time points (ranging from -250 ms to 700 ms relative to tactile stimulus onset in steps of 20 ms), frequencies (frequency bins ranging from 2 to 40 Hz in steps of 2 Hz)

and electrodes (Maris & Oostenveld, 2007). Because this test does not trivially generalize to ANOVAs, we first tested for a three-way interaction between Group, Attention, and Posture by conducting a CBPT over the interaction effects of Attention and Posture between the two participant groups. Subsequently, CBPTs were performed separately for each participant group's interaction between Posture and Attention. When this group-wise analysis yielded a significant interaction between Posture and Attention, separate CBPT were performed to compare individual conditions. Otherwise, when the group-wise analysis did not reveal a significant interaction between Posture and Attention, CBPT were conducted to test for main effects of Posture and Attention.

4.2.5 Source reconstruction

To reconstruct the neuronal sources of effects observed at the sensor level, we applied a beamforming technique in the frequency domain (Gross et al., 2001; Liljeström et al., 2005) to estimate power values at points of a 7 mm grid, which was evenly distributed throughout the brain (Schubert et al., 2015).

The power change for each grid point between baseline activity and post-stimulus activity was decibel scaled [$P = 10 * (\log_{10}(P_{\text{poststimulus}}) - \log_{10}(P_{\text{baseline}}))$]. Frequency range and time interval for beamforming were determined for each analysis by the results obtained at the sensor level, i.e. using the time and the frequencies showing the largest differences between conditions. Differences between conditions were statistically tested in source space using a cluster-based permutation test (Maris & Oostenveld, 2007).

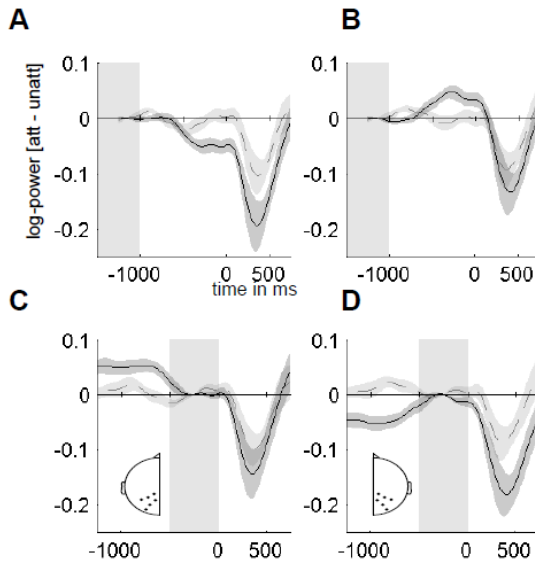


Figure 4.1. Difference waves of alpha-band activity (10–14 Hz) over time in the sighted group with a pre-cue baseline (A, B) and a pre-stimulus baseline (C, D). Traces are difference waves of activity in trials with attended stimuli minus activity in trials with unattended stimuli at posterior parietal electrodes (marked on the semi-head montages in C and D), for the uncrossed (solid black) and crossed (grey dashed) postures. Left column (A, C): contralateral; right column (B, D): ipsilateral hemisphere, relative to tactile stimulation. Shaded rectangles mark the time window used as baseline. Note that, in A and B, alpha-band activity is lateralized with uncrossed hands already during the cue-target interval, for which we previously reported posture-related alpha-band lateralization. This difference in pre-stimulus activity is eliminated for the current analysis by baselining to the time interval directly prior to stimulation, as illustrated in (C, D). Shaded areas around activity traces represent the standard error of the mean.

4.3 Results

4.3.1 Behavioral results

As reported previously (Röder et al., 2008; Schubert et al., 2015) and depicted in Fig. 3.7A, posture significantly influenced d-prime scores, that is, hit minus false alarm rates, only in the sighted group (Group – Posture interaction: $F(1, 22) = 5.87$, $p = 0.024$), with higher d'-scores in the sighted with uncrossed than with crossed hands ($t(11) = 3.56$, $p = 0.004$). In the blind group, target detection rates 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 ($t(22) = 0.98$, $p = 0.337$).

4.3.2 Oscillatory activity following tactile stimulation: sighted group

We analyzed the power of oscillatory activity in sighted and congenitally blind participants following the presentation of a tactile stimulus presented to attended versus unattended hands with uncrossed and crossed hand postures.

Interaction effects of Attention and Posture (i.e., the difference between oscillatory activity following attended and activity following unattended stimuli with uncrossed hands minus the difference between oscillatory activity following attended and following unattended stimuli with crossed hands) were significantly different between groups (CBPT: $p < 0.001$). This difference was most pronounced for frequencies around 12 Hz in the time interval 400–500 ms post-stimulus at posterior parietal electrodes ipsilateral to stimulation, with a larger interaction in the sighted than in the blind group. Consequently, we investigated whether and how Attention and Posture modulated oscillatory activity separately for each group.

In the sighted group, we observed an interaction between Posture and Attention (CBPT: $p = 0.006$) that was most pronounced for a frequency range around 12 Hz in the time interval 400–600 ms (Fig. 4.2AB, i), with a larger attention effect with uncrossed than crossed hands.

Although this effect was observable at nearly all electrodes, it was largest at ipsilateral parietal–occipital electrodes. Time-frequency representations of the electrode showing the largest interaction between Posture and Attention are shown in Fig. 4.2B. This electrode is near P3/4 in the 10-10 system, and it is marked with an asterisk on the

topographies in Fig. 4.2A. Attended stimuli elicited a suppression of activity in the alpha- and beta-bands when compared to unattended stimuli (Figs. 4.2AB, a–f, 4.3). This attentional suppression effect was evident for both uncrossed and crossed hand postures (Fig. 4.2AB,c, f; CBPT: $p < 0.001$ and $p = 0.004$, respectively), but was smaller with crossed than with uncrossed hands in the alpha-band (Fig. 4.2AB, i). Following attended stimuli, suppression of alpha-band activity was stronger with uncrossed than with crossed hands (Fig. 4.2AB, g; CBPT: $p = 0.006$). This result pattern of hand crossing effects was reversed for unattended stimuli: suppression of alpha-band activity was stronger with crossed than with uncrossed hands (Fig. 4.2AB, h; CBPT: $p = 0.018$). Both of these effects were most pronounced at ipsilateral occipital and parietal electrodes.

4.3.3 Oscillatory activity following tactile stimulation: blind group

Oscillatory activity in the congenitally blind group differed markedly from that in the sighted group. A CBPT failed to reveal a significant interaction between attention and posture (CBPT: $p = 0.106$). A subsequent CBPT revealed a main effect of attention on oscillatory activity (CBPT: $p = 0.006$; Figs. 4.4, 4.5). Specifically, activity was enhanced following attended compared to unattended stimuli for a range of frequencies including alpha- and beta-bands at contralateral frontal and central electrodes. Posture only marginally modulated oscillatory activity (CBPT: $p = 0.060$). This marginal modulation was most prominent in the alpha-band frequency range at 12 Hz around 470 ms poststimulus at contralateral temporal electrodes (approximately T7/8 in the 10–10 system), with a stronger suppression in the crossed than in the uncrossed posture.

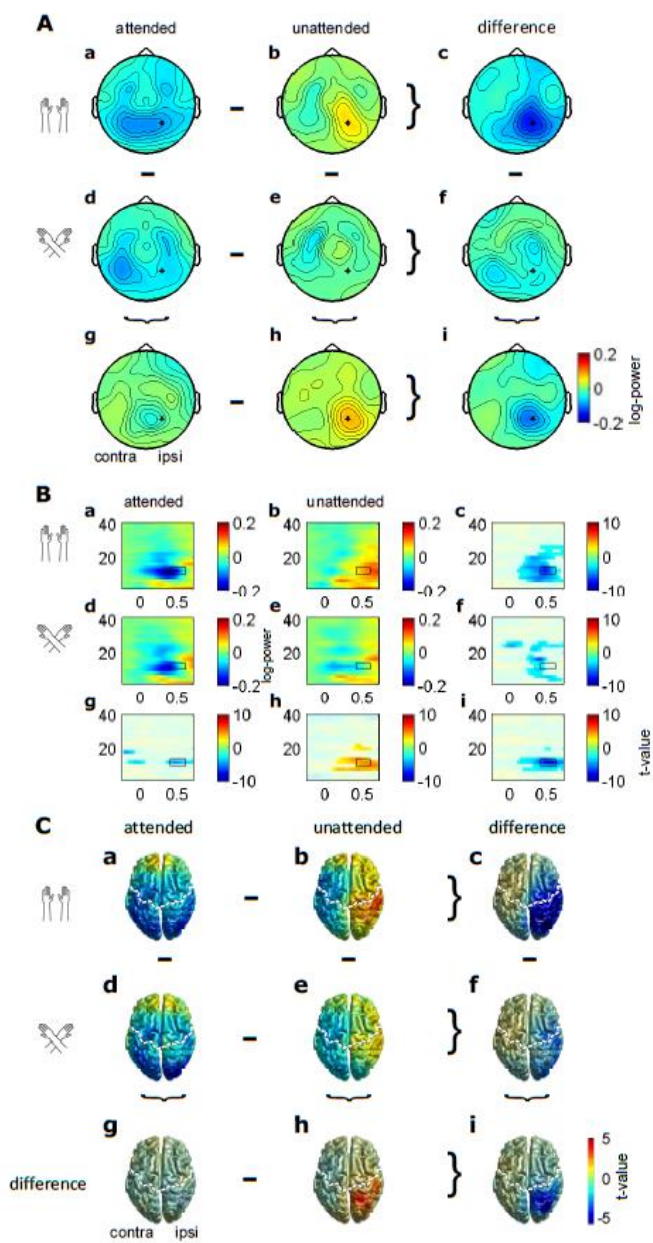


Figure 4.2. Alpha-band activity in the sighted group. **A.** Topographies of alpha-band activity (10-14 Hz, 400 to 600 ms, marked with black rectangle in **B**) with uncrossed (**a, b**) and crossed hands (**d, e**) following attended (**a, d**) and unattended (**b, e**) stimuli. **c, f, g, h.** Difference topographies for attention effects with uncrossed (**c**) and crossed (**f**) hands, and for posture effects following attended (**g**) and unattended (**h**) stimuli. **i.** Topography of the interaction between attention and posture. Maps are displayed as if all stimuli were presented to the right hand, i.e., the left hemisphere is contralateral to stimulation with respect to anatomy (not side of space). **B.** Time-frequency representation of the electrode showing the largest interaction between posture and attention (marked with an asterisk in **A**, approximately P3/4 in the 10-10 system) with uncrossed (**a, b**) and crossed hands (**d, e**) following attended (**a, d**) and unattended (**b, e**) stimuli. Unmasked areas in **c, f, g, h,** and **i** indicate significant differences between attention conditions with uncrossed (**c**) and crossed hands (**f**), between posture conditions following attended (**g**) and unattended stimuli (**h**), and a significant interaction between posture and attention (**i**) (cluster-based permutation test, $p < 0.05$). **C.** Neural sources of alpha-band activity. Alpha-band activity (12 ± 2 Hz, $t = 400$ ms) with hand uncrossed (**a, b**) and crossed (**d, e**) following attended (**a, d**) and unattended (**b, e**) stimuli. Source statistics are shown for the interaction effect between posture and attention (**i**), for effects of posture following attended (**g**) an unattended (**h**) stimuli, and for effects of attention with uncrossed (**c**) and crossed (**f**) hands. Significant clusters in **c, f, g-i** are unmasked. The left (right) hemisphere is contralateral (ipsilateral) to the stimulated hand. The white dashed line denotes the central sulcus.

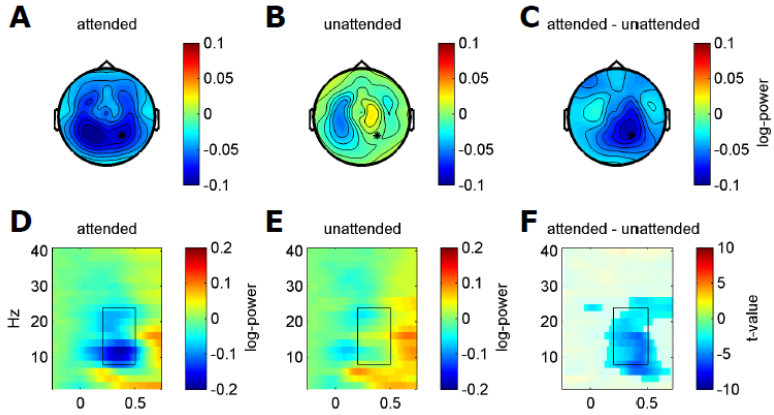


Figure 4.3. Sighted group, main effect of Attention. **A–C.** Topographies of alpha- and beta-band activity (8–24 Hz, 200–500 ms, marked with black rectangle in **D–F**) following attended (**A**) and unattended (**B**) stimuli and difference topography (**C**). **D–F.** Time-frequency representation of the electrode marked with an asterisk in **A–C** (approximately P3/4 in the 10–10 system) following attended (**D**) and unattended (**E**) stimuli and statistical difference between attention conditions (**F**) with significant clusters being unmasked (CBPT: $p < 0.001$).

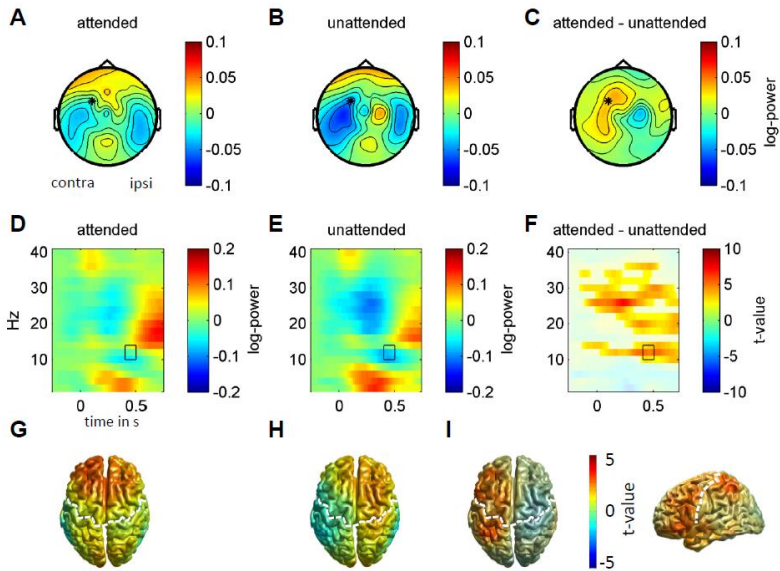


Figure 4.4. Alpha-band activity in the blind group. **A–B.** Topographies of alpha-band activity (10–14 Hz, 400 to 500 ms, marked with black rectangle in **D–F**) following attended (**A**) and unattended (**B**) stimuli. **C.** difference topography of (**A**) minus (**B**). **D–E.** Time-frequency representation (TFR) of the electrode marked with an asterisk in **A–C** (approximately FC3/4 in the 10–10 system) following attended (**D**) and unattended (**E**) stimuli. **F.** TFR of statistical difference between attention conditions with significant clusters being unmasked (**F**). **G–I.** Source reconstruction of alpha-band activity elicited by attended (**G**) and unattended (**H**) stimuli and the attention effect (**I**), view from above (left) and lateral view of the contralateral hemisphere (right), significant clusters are unmasked (CBPT: $p = 0.005$). The white dashed line denotes the central sulcus. The left (right) hemisphere is contralateral (ipsilateral) to the stimulated hand in all panels.

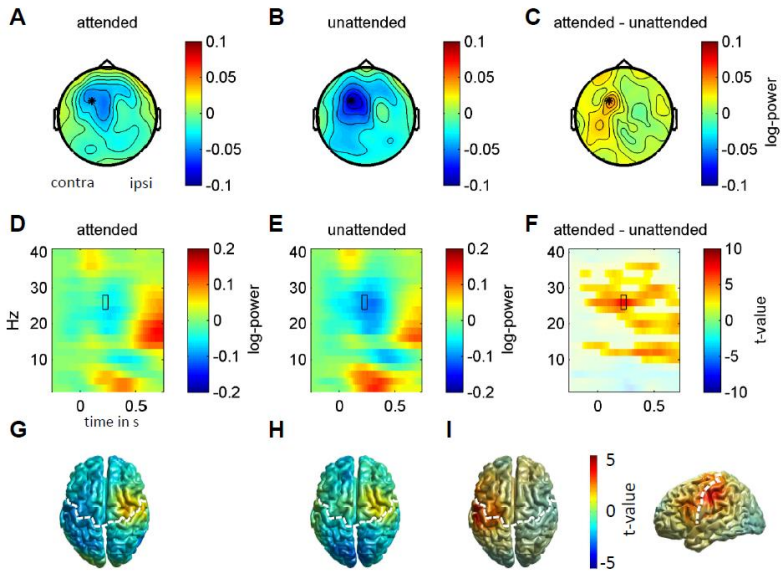


Figure 4.5. Beta-band activity in the blind group. **A-B.** Topographies of beta-band activity (24-28 Hz, 200 to 250 ms, marked with black rectangle in **D-F**) following attended (**A**) and unattended (**B**) stimuli. **C.** difference topography of (**A**) minus (**B**). **D-E.** Time-frequency representation (TFR) of the electrode marked with an asterisk in **A-C** (approximately FC3/4 in the 10-10 system) following attended (**D**) and unattended (**E**) stimuli. **F.** TFR of statistical difference between attention conditions with significant clusters being unmasked (**F**). **G-I.** Source reconstruction of beta-band activity elicited by attended (**G**) and unattended (**H**) stimuli and the attention effect (**I**), view from above (left) and lateral view of the contralateral hemisphere (right), significant clusters are unmasked (CBPT: $p = 0.044$). The white dashed line denotes the central sulcus. The left (right) hemisphere is contralateral (ipsilateral) to the stimulated hand in all panels.

4.3.4 Neuronal sources of posture and attention effects

We followed up significant effects in the two groups by identifying their neural sources using a beamforming approach. For the sighted group, we investigated the neuronal sources of the difference between attention effects with uncrossed and crossed postures. Following attended compared to unattended stimuli with uncrossed hands, alpha-band activity (10–14 Hz) was significantly suppressed in a broad area of the ipsilateral hemisphere relative to the stimulated hand, including in sensorimotor as well as parieto–occipital regions (CBPT: $p < 0.001$; see Fig. 4.2C, c). Consistent with the results of the sensor-level analysis, the attention-related suppression effect was still present, yet reduced, when the hands were crossed (CBPT: $p = 0.003$; see Fig. 4.2C, f). This interaction between attention and posture originated from ipsilateral posterior parietal cortex (Fig. 4.2C, i; $p = 0.007$; absolute maximum at MNI coordinate [30 -81 56]), extending into angular gyrus, S1, S2, and occipital regions.

In the blind group, we had observed a broad-frequency effect of attention at the sensor level, but with individual activity peaks for alpha-band and beta-band effects. We therefore beamformed the alpha-band (12 Hz \pm 2 Hz) at 500 ms, and beta-band activity (26 Hz \pm 2 Hz) at 250 ms after stimulation. Alpha-band activity in the contralateral hemisphere was enhanced for attended relative to unattended stimuli ($p = 0.005$; maximal difference at MNI [-44 -56 58]). This effect was broadly distributed over contralateral posterior-parietal cortex, S1, middle and inferior temporal areas, premotor and motor regions as well as the insula and dorso-lateral prefrontal cortex (Fig. 4.4G–I). Similarly beta-band activity was enhanced following attended relative to unattended stimuli in the contralateral hemisphere. However, the beta-band effect was more spatially confined than that in the alpha-band, covering a region including primary somatosensory cortex and motor regions (Fig. 4.5G–I, MNI coordinate of the maximal difference [-62 -8 24]) (CBPT: $p = 0.036$).

4.4 Discussion

The present study investigated whether alpha-band activity is related to the external spatial coding of touch and is, therefore, modulated by hand posture. A modulation by hand posture during stimulus processing would indicate a general role of alpha-band activity for the spatial processing beyond the orienting of attention (Chapter 3; Schubert et al.,

2015). Congenitally blind individuals, who, in contrast to the sighted, do not routinely integrate postural information during the processing of touch (Röder et al., 2008, 2004), served as an additional model to investigate the spatial roles of alpha- and beta-band activity during tactile processing. The analysis focused on oscillatory EEG activity following attended and unattended tactile stimuli delivered to uncrossed and crossed hands in sighted and congenitally blind participants.

In the sighted group, spatially attended tactile stimuli elicited stronger alpha- and beta-band suppression in the ipsilateral parietal occipital cortex than unattended stimuli when the hands were uncrossed. In contrast, in the congenitally blind group, attended compared to unattended tactile stimuli elicited enhanced oscillatory activity in the alpha- and beta-band ranges in contralateral fronto-central cortex with uncrossed hands. In the sighted group, hand crossing attenuated attentional effects on alpha-band activity in a widespread network within the ipsilateral hemisphere, with a maximum in posterior parietal cortex, extending to occipital as well as primary and secondary somatosensory areas. Much in contrast, posture did not significantly modulate attention-related oscillatory activity in the blind group.

4.4.1 Attentional modulations of oscillatory activity in sighted individuals with uncrossed hands

In sighted participants, tactile stimuli have been reported to elicit stronger and longer-lasting alpha- and beta-band suppression in bilateral parieto-occipital cortex when they are attended than when not (Bauer et al., 2006). In line with these findings, we observed suppression of parieto-occipital oscillatory activity in the alpha- and beta-bands with uncrossed hands. Specifically, attended stimuli suppressed activity in bilateral posterior parietal cortex (Figs. 4.2AC, a), whereas unattended stimuli suppressed contralateral, but enhanced ipsilateral activity (Figs. 4.2AC, b). These modulations resulted in an ipsilateral attention effect when contrasting attended versus unattended stimuli. Given that alpha-band activity is thought to decrease in engaged regions, and to increase in disengaged regions (Jensen & Mazaheri, 2010), this observation suggests that the ipsilateral hemisphere is more strongly involved in the processing of attended than of unattended tactile stimuli. Consistent with our results, stronger effects of transient tactile attention in the ipsilateral hemisphere have been observed in several ERP studies (e.g.

Eardley & van Velzen, 2011; Heed & Röder, 2010; Röder et al., 2008). Moreover, modulation of stimulus-related oscillatory activity ipsilateral to tactile stimulation has been reported to vary with the degree to which attention has built up over time (van Ede et al., 2013): The longer the cue–target interval, that is, the more time was available for attentional preparation, the stronger was the stimulus-induced suppression of alpha- and beta-band activity in the ipsilateral somatosensory cortex. Adopting the view that in our paradigm time for attentional preparation was similarly available as in the long intervals in that study (i.e. 1000 ms), the ipsilateral hemisphere may have been actively recruited during tactile stimulus processing when the stimulus occurred at the location to which attention was oriented to (van Ede et al., 2013). However, the present observation of an ipsilateral attention effect contrasts with the bilateral effect of tactile attention on alpha and beta activity reported previously (Bauer et al., 2006). At least two aspects may account for these differences in lateralization between the present and earlier reports. First, attention was directed transiently, that is, trial by trial, in the present study, whereas Bauer and colleagues (2006) used a sustained attention paradigm. Both transient and sustained attentional orienting have been shown to modulate somatosensory ERPs in different ways. Specifically, sustained attention changes the amplitude of earlier ERPs (including the N80) than transient attentional orienting in trial-by-trial cuing paradigms (earliest attention effects for the P100 and N140) (Eimer & Forster, 2003). Because the N80 has a strong contralateral topography, it has been suggested that sustained attention affects tactile processing in contralateral S1, but that transient attention mainly influences higher order areas such as S2 (Eimer & Forster, 2003). In analogy to this proposal, we speculate that the effects of transient attention were mainly generated in the higher-order areas. Second, participants had their eyes closed in the present study to match sensory input between sighted and blind individuals. In contrast, participants had their eyes open in previous studies (Bauer et al., 2006). Closing the eyes has, furthermore, been reported to affect BOLD activity in the left intraparietal sulcus and superior occipital gyrus during tactile attentional processing (Macaluso, Frith, & Driver, 2000).

4.4.2 Hand crossing reduces attention-related alpha-band effects in the sighted

In the sighted, anatomical and external reference frames concurrently modulated oscillatory brain activity during the orienting of attention (Schubert et al., 2015) as well as in the context of movement planning (Buchholz et al., 2011, 2013). Moreover, several ERP studies have indicated the concurrent use of both reference frames during tactile stimulus processing. Attention effects on somatosensory ERPs are reduced in the time range of the P100, the N140, and 200-300 ms post-stimulus for crossed as compared to uncrossed hands (Eardley & van Velzen, 2011; Eimer et al., 2003; Gherri & Forster, 2012; Heed & Röder, 2010). For the spectral domain, the present study reveals that alpha-band activity is susceptible to information from an external spatial reference frame not only for attentional orienting while expecting a tactile stimulus, but additionally during genuine tactile stimulus processing. Hand crossing led to a reduction of the attention-related suppression of alpha-band activity over ipsilateral posterior parietal cortex. Pre-stimulus alpha-band lateralization has been shown to predict subsequent tactile performance, with higher lateralization coinciding with better performance (Haegens et al., 2011). Alpha-band lateralization, therefore, appears to play an important role in setting the state of sensory regions to optimize subsequent processing (Haegens et al., 2011). Because alpha-band lateralization during the cue–target interval is reduced by hand crossing (Chapter 3; Schubert et al., 2015), attentional orienting may have been less efficient with crossed than with uncrossed hands, which in turn might result in degraded task performance. The present effect of hand crossing on alpha-band activity would thus be explained by a reduced signal to noise level of relative hemispheric activation, that is, a lower attentional suppression of ipsilateral alpha-band activity with crossed than uncrossed hands.

4.4.3 Brain regions involved in external stimulus mapping

It is currently unknown which brain regions make up the network for the remapping of touch. Source reconstruction revealed that posture affected a range of regions in the ipsilateral cortex in the present study (Fig. 4.2C, i) with local foci in posterior parietal cortex close to the intraparietal sulcus (IPS), angular gyrus, S1, and S2. This result is consistent with enhanced fMRI activation in the insular, temporal, and parietal cortex during tactile tasks with crossed compared to uncrossed

hands (Takahashi, Kansaku, Wada, Shibuya, & Kitazawa, 2013). Together, these regions might form a network that codes hand location in external space. Accordingly, tactile remapping does not appear to be a function constrained to a single brain region, but rather depends on the interaction of several brain regions.

There was considerable overlap between the posterior-parietal regions that were associated with external spatial coding in the present study, and those of our previous report that investigated attentional orienting in anticipation of tactile stimulation. The consistency of regions involved in external coding during pre- and post-stimulus phases suggests a general, task-independent role of the intraparietal sulcus in spatial processing. Indeed, activity during movement planning to remembered tactile targets, too, considerably overlapped with activity of the present study (Buchholz et al., 2011, 2013). The IPS has been suggested to contain supramodal spatial maps (Y. E. Cohen & Andersen, 2002; Graziano & Cooke, 2006; Schlack et al., 2005). Moreover, it is thought to be involved in the remapping of anatomical coordinates of touch into external space (Azañón et al., 2010; Bolognini & Maravita, 2007; Renzi et al., 2013). Furthermore, entrainment of this region with 10 Hz repetitive TMS has been reported to enhance tactile discrimination in the ipsilateral external space (Ruzzoli & Soto-Faraco, 2014), suggesting that alpha-band activity plays a causal role in the representation of touch in an external reference frame. Moreover, posture affected alpha-band activity in the angular gyrus, a region that has been associated with the perception of the own body (Blanke, Ortigue, Landis, & Seeck, 2002; Rusconi, Walsh, & Butterworth, 2005). Electrical stimulation of the right angular gyrus can lead to illusory limb shortening and movements (Blanke et al., 2002). Disturbing the left angular gyrus by means of repetitive TMS disrupted finger gnosis (Rusconi et al., 2005), and lesions of the angular gyrus have been suggested to be at the core of the clinical deficit of spatial neglect (Mort et al., 2003), a disorder that affects both body perception and attention. Hand crossing, as used in the present study, changes the relations between body parts and is thus likely to activate processes involved in body perception. Body-related information may then be fed to IPS via known functional anatomical connections from angular gyrus to IPS (Uddin et al., 2010). Finally, posture-related alpha-band modulation was evident in opercular cortex and S2 (Eickhoff, Amunts, Mohlberg, & Zilles, 2006). Activity in the right frontal operculum has been associated with the strength of the rubber

hand illusion (Tsakiris, Costantini, & Haggard, 2008), a phenomenon that affords an adjustment of the perceived location of the hand based on visual spatial cues. In the present study, hand crossing may have similarly activated this cortical region to update hand location. S2 has been identified as a likely constituent of a tactile remapping network, as it showed externally coded oscillatory activity during motor planning to tactile targets (Buchholz et al., 2013). The external coding of tactile stimuli has furthermore been suggested to involve S2 based on the timing of crossing effects on attention-related somatosensory ERPs (Heed & Röder, 2010), paired with the finding that top-down connections exist from IPS to S2 in macaques (Lewis & Van Essen, 2000), suggesting that remapped information may be routed from posterior parietal to somatosensory cortex.

4.4.4 Attention, but not posture, modulates touch-related alpha- and beta-band activity in congenitally blind individuals

There is abundant evidence that congenitally blind individuals preferably use an anatomical rather than external spatial code for touch when the context does not require the use of an external reference frame, indicating that developmental vision critically influences the spatial coding of touch (Crollen, Albouy, Lepore, & Collignon, 2013; Röder et al., 2008, 2004). For instance, attention-related somatosensory ERP effects are reduced by hand crossing in the range of the 96-120 ms and 160-250 ms poststimulus in sighted, whereas in congenitally blind individuals somatosensory ERPs 160-250 ms poststimulus are modulated by attention, but not by hand crossing (Röder et al., 2008). Similarly, the lateralization of posterior-parietal alpha-band activity during the orienting of attention is attenuated by hand crossing in sighted, but not in blind individuals (Schubert et al., 2015). Although attention modulated oscillatory alpha- and beta-band activity during tactile processing in the blind group, this effect was not significantly modulated by hand posture. There was a trend, however, that contralateral activity in the alpha-band range was more suppressed with uncrossed than with crossed hands in the blind group, irrespective of the attention condition. This trend suggests that hand posture may not be completely neglected by blind individuals, though the postural influence appears to be much smaller than in the sighted (Eardley & van Velzen, 2011). The differential effect between groups matches the behavioral results of the present experiment, with an enhanced

performance with uncrossed compared to crossed hands in the sighted, but not in the blind group. This difference in the modulation of alpha-band activity in the sighted highlights the role of alpha-band activity during spatial tactile processing.

The spatial signature of the blind group's attention-related alpha- and beta-band modulation markedly differed from that of the sighted. Whereas processing of attended versus unattended tactile stimuli was associated with suppression of ipsilateral parietal alpha- and beta-band activity in the sighted group, it was related to fronto-central power enhancement for both alpha- and beta-band activity in the congenitally blind group. Source reconstruction suggested that the different patterns of activity observed on the electrode level were due to an involvement of vastly different regions in the two groups: ipsilateral posterior parietal cortex in the sighted group, and contralateral fronto-central cortex, including the somatosensory cortex, in the blind group. Thus, both the oscillatory mechanisms – relative suppression vs. relative enhancement – as well as the mediating brain regions involved in the coding of tactile attention, appear to differ fundamentally in dependence of developmental vision. The posterior-parietal regions relevant in the sighted group have previously been associated with the coding of an external reference frame (Buchholz et al., 2011, 2013). In contrast, the regions activated in the blind group included primary somatosensory regions, whose homuncular organization reflects its anatomical coding. In addition, however, it is noteworthy that sighted and blind individuals recruited different regions of the fronto-parietal network that is thought to mediate top-down modulation of attentional processing (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Marshall, O'Shea, Jensen, & Bergmann, 2015), with sighted participants recruiting parietal, and blind participants recruiting frontal regions. Several studies have proposed that sighted and blind individuals use different coding strategies in the context of tactile attention (Collignon et al., 2006; Forster, Eardley, & Eimer, 2007; Röder et al., 2008; Van Velzen, Eardley, Forster, & Eimer, 2006). In the blind group, the stronger contralateral suppression of alpha- and beta-band activity following unattended compared to attended stimuli may reflect a coding strategy in which tactile input at irrelevant locations is processed more thoroughly than input at an attended location. An irrelevant stimulus appearing at an attended location would then be processed more efficiently than an irrelevant stimulus at an unattended location. In the

present study, the differential lateralization of attention-related effects in tactile processing in sighted and blind individuals may, therefore, reflect such different strategies between groups.

To conclude, we have demonstrated that alpha-band activity is closely associated with external spatial coding during the processing of tactile stimulation, evident in the attenuation of ipsilateral attention effects in the alpha-band by hand crossing in sighted adults.

The similarity of the modulatory influence of hand posture on activity during stimulus-related processing and on activity during the orienting of attention prior to stimulation attests alpha-band activity a general role in external-spatial coding of tactile information. This conclusion is further corroborated by the absence of an external-spatial modulation of alpha-band activity in congenitally blind humans. Beyond differences between sighted and blind individuals in the role of the alpha-band to code external space, the brain regions recruited by the alpha- and beta-rhythm were fundamentally different between the two groups. This finding highlights the critical influence of developmental vision on the emergence of oscillatory activity mediating tactile spatial and attentional functions.

Chapter 5:
**Task context effects on tactile
reference frame weighting in sighted
and congenitally blind humans**

5.1. Introduction

One of the brain's most important processing strategies is the integration of information originating from different sources, such as multiple sensory channels. Much research has attempted to uncover how these multiple sources of information are integrated into a coherent percept (Alais & Burr, 2004; Angelaki, Gu, & DeAngelis, 2009; Ernst & Banks, 2002; Körding & Wolpert, 2004; Landy, Maloney, Johnston, & Young, 1995; Sober & Sabes, 2005; Trommershauser, Körding, & Landy, 2011). For tactile localization, too, several information sources are integrated, and so this process has been scrutinized to investigate information integration within and across the senses. Tactile localization has been suggested to be a two-step process (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015). When tactile information first arrives in the cortex, it is initially encoded relative to the skin in an anatomical reference frame, reflected in the homuncular organization of the somatosensory cortex (Penfield & Boldrey, 1937), and then, in a first step, remapped into an external reference frame. By merging this skin-based spatial information with proprioceptive, visual, and vestibular signals, the brain derives an external spatial location, a process usually referred to as tactile remapping (Clemens et al., 2011; Driver & Spence, 1998; Heed, Buchholz, et al., 2015; Holmes & Spence, 2004; Maravita et al., 2003). The term 'external', in this context, denotes a spatial code that abstracts from the original location, but may nevertheless be egocentric, and, as such, be anchored to eyes, head, or torso (Heed, Buchholz, et al., 2015). In a second step, information of the two reference frames is integrated, presumably to derive an superior tactile location estimate (Badde, Heed, et al., 2014, 2015; Badde, Röder, & Heed, 2014; Badde, Röder, et al., 2015). For sighted individuals, this integration of different tactile codes appears to be mandatory (Azañón, Camacho, & Soto-Faraco, 2010; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001), but their relative weight is subject to change depending on current task demands: external spatial information is weighted more strongly when task instructions emphasize external spatial aspects (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015), in the context of movement (Gherri & Forster, 2012a, 2012b; Heed, Möller, et al., 2015; Hermosillo et al., 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012), and in the context of frequent posture changes (Azañón et al., 2015; for a review see Badde & Heed, in press).

Thus, tactile localization estimation depends on flexibly weighted integration of spatial reference frames.

Moreover, tactile localization critically depends on visual input from birth on. Misaligning anatomical and external spatial reference frames by crossing the hands over the midline (i.e., the left hand occupies the right external space) reportedly impairs tactile localization compared to an uncrossed hands posture in sighted, but not in congenitally blind individuals (Collignon et al., 2009; Röder et al., 2004). Similarly, hand crossing reportedly attenuates attention-related effects on somatosensory event-related potentials (ERP) between 96 and 250 ms poststimulus in sighted, but not in congenitally blind individuals (Röder et al., 2008). Together, these previous studies indicate that, contrary to sighted individuals, congenitally blind may not by default integrate external information with skin-based information. Yet, recent studies have cast doubt on the generality of this conclusion. For instance, it has been demonstrated that congenitally blind individuals used external along with anatomical coding when tactile stimuli had to be localized while making bimanual movements (Heed, Möller, et al., 2015). In addition to tactile localization tasks, evidence from a bimanual coordination task, too, indicates that congenitally blind individuals do integrate external spatial information: when they moved their fingers symmetrically, this symmetry appeared to be encoded relative to external space rather than according to anatomical parameters such as the involved muscles (Heed & Röder, 2014). Moreover, the mental representation of time has been suggested to be encoded relative to external space in early blind individuals and, possibly, to be related to left-right movements during Braille reading (Bottini et al., 2015). These studies imply that congenitally blind humans, like the sighted, integrate spatial information coded in different reference frames according to a weighting scheme (Badde, Heed, et al., 2015). Furthermore, although weighting preferences appear to differ between these two groups, movement contexts appear to induce stronger weighting of external spatial information in both sighted and congenitally blind individuals.

Besides movement context, task demands have been demonstrated to be an additional factor that can modulate the weighting of spatial information in tactile localization of sighted individuals. For instance, tactile temporal order judgments (TOJ), that is, the decision which of two tactile locations was stimulated first, are sensitive to a conflict between anatomical and external locations that arises when stimuli are

applied to crossed hands. These crossing effects, indicative of the weighting of the two tactile codes, were modulated differently when a secondary task accentuated anatomical versus external space (Badde, Röder, et al., 2015). Another possibility to study spatial tactile processing is to test how task-irrelevant distractors interfere with tactile localization (Spence et al., 2004). For instance, elevation judgements of tactile stimuli on the hands are faster and more accurate when a visual distractor is simultaneously presented at a congruent than at an incongruent elevation (Spence et al., 2000). Similarly, tactile distractors presented to one hand interfere with elevation judgements about simultaneously presented tactile target stimuli presented at congruent locations of the other hand (Gallace et al., 2008; Soto-Faraco et al., 2004). In such tasks, spatial congruency can be defined in two ways: congruent in an anatomical reference frame, that is, both stimuli occur at corresponding skin locations, or congruent in an external reference frame, that is, both stimuli occur at corresponding elevations. If both hands are held in the same posture, e.g., with both palms facing down, anatomical and external congruencies correspond to each other. However, hand posture can be manipulated in a way that the palm of one hand faces up and the other down. In this case, two tactile stimuli, which are presented at the top of each hand, are presented at different anatomical skin location and, thus, anatomical and external congruencies contradict each other. A comparison of congruency effects between these postures then provides a measure of the weighting of anatomical and external tactile codes. This weighting has been shown to be subject to task context effects as well: when task instructions required participants to report tactile elevation relative to their external rather than to their anatomical location spatial congruency modulated performance in an external reference frame (Gallace et al., 2008). Yet, whether congruency effects were encoded relative to anatomical or relative to external space was modifiable by both task instructions and response modalities (Gallace et al., 2008). This suggests that the weighting of anatomical and external spatial information in the tactile congruency task was flexible, and was modulated by task requirements. In congenitally blind humans, indirect evidence is currently available as to whether task instructions may modulate spatial tactile integration in a similar way as in sighted individuals. Two very similar studies have investigated tactile spatial coding in early and congenitally blind humans by examining somatosensory ERPs elicited by tactile stimulation in

different hand postures. Both studies asked participants to report infrequent tactile target stimuli on a pre-cued hand, but observed contradicting results: One study reported an attenuation of attention-related somatosensory ERPs between 140 and 300 ms poststimulus to non-target stimuli with crossed compared to uncrossed hands (Eardley & van Velzen, 2011), suggesting that external location had affected tactile spatial processing in blind participants. The other study (Röder et al., 2008), in contrast, did not observe any modulation of attention-related somatosensory ERPs by hand posture and concluded that congenitally blind humans do not, by default, use external spatial information for tactile localization. The two studies differed in how participants were instructed about the to-be-monitored location. In the first study, a cue indicated the task-relevant side relative to external space in each trial (Eardley & van Velzen, 2011). In the second study, in contrast, cueing referred to the task-relevant hand, independent of hand location in external space (Röder et al., 2008). Thus, task instructions may modulate how anatomical and external information is weighted in congenitally blind individuals as they do in the sighted. Additional evidence for weighted integration of anatomical and external tactile codes in congenitally blind humans comes from a recent study employing the tactile TOJ task (Badde, Ley, & Röder, 2016). When congenitally blind individuals indicated the location of the first touch with respect to the side of space, that was stimulated first, some participants showed a hand crossing effects, suggesting an integration of external spatial information.

In contrast, when they localized the first touch with respect to the hand, no significant hand crossing effects emerged in previous findings (Röder et al., 2004). Moreover, when TOJ of two tactile stimuli were randomly interleaved with TOJ of two auditory stimuli and crossmodal TOJ of one tactile and one auditory stimulus, all congenitally blind participants showed a hand crossing effect in tactile TOJ (Badde et al., 2016). Presumably, the auditory stimuli, originating from loudspeakers positioned in front of each hand, created a task context that triggered increased weighting of external spatial codes of touch.

Here, we investigated the weighting of anatomical and external reference frames by means of an adapted version of the tactile congruency task (Gallace et al., 2008; Soto-Faraco et al., 2004). Sighted and congenitally blind participants localized vibro-tactile target stimuli, presented randomly on the palm or back of one hand, while ignoring a

vibro-tactile distractor on the palm or back of the other hand. Thus, the distractor could appear at an anatomically congruent or incongruent location. Hand posture was varied to allow investigation of the weighting of the involved spatial reference frames, with either both palms facing downwards, or one palm downwards and the other upwards. With differently oriented hands, anatomically congruent stimuli were incongruent in external space and vice versa. Thus, misaligning spatial reference frames by orienting the hands in different directions allows investigating whether tactile congruency effects are encoded relative to anatomical or to external spatial locations.

We introduced two experimental manipulations to investigate the role of task demands on the weighting of anatomical and external spatial information. First, every participant performed the task under two different sets of instructions: In one session, responses were instructed anatomically, that is, with respect to palm or back of the hand. In a second session, responses were instructed externally, that is, with respect to upper and lower locations in space. We hypothesized that task instructions would emphasize the weighting of the corresponding reference frame. This means that with differently oriented hands (that is, when anatomical and external reference frames are misaligned) the size, or even direction, of congruency effects should depend on task instructions.

With the second manipulation, we aimed at corroborating previous results suggesting that movement planning and execution as well as frequent posture change lead to an emphasized weighting of external spatial information (Azañón et al., 2015; Gherri & Forster, 2012a, 2012b; Heed, Möller, et al., 2015; Hermsillo et al., 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012). Accordingly, we hypothesized that frequent posture changes would increase the weight of the external reference frame in a similar way for the spatial coding of congruency in the present task. To this end, participants either held their hands in a fixed posture for an entire experimental block, or they changed their hand posture in a trial-by-trial fashion. Again, with differently oriented hands, changes in the weighting of anatomical and external spatial information would be evident in a modulation of tactile congruency effects; frequent posture changes, compared to a blockwise posture change, should induce an increased weighting of external information. This would show in a decrease of anatomical congruency effects under anatomical instructions and in an increase of external congruency

effects under external instructions. The weighting of external spatial information reportedly depends on the sensory experiences during early childhood (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013). Studying how congenitally blind adults weight spatial information for tactile localization, thus, offers a model to investigate whether visual deprivation from birth on prevents the default integration of anatomical and external spatial information or whether anatomical and external spatial information is integrated, but with altered integration weights.

5.2. Methods

We follow open science policies and, thus, report how we determined the sample size, all experimental manipulations, all exclusions of data, and all evaluated measures of the study.

5.2.1. Participants

The size of our experimental groups was constrained by the availability of congenitally blind volunteers; we invited every suitable participant we identified within a period of 6 months. Group size is comparable to that of previous studies that have investigated spatial coding in the context of tactile congruency. We report data from sixteen congenitally blind participants (8 female, 15 right handed, age: $M = 37$, $SD = 11.6$, range: 19 to 53) and from a matched control group of sixteen blindfolded sighted participants (8 female, all right handed, age: $M = 36$, $SD = 11.5$, range: 19 to 51). All sighted participants had normal or corrected-to-normal vision. Blind participants were visually deprived from birth due to anomalies in peripheral structures resulting either in total congenital blindness ($n = 6$) or in minimal residual light perception ($n = 10$). Peripheral defects included binocular anophthalmia ($n = 1$), retinopathy of prematurity ($n = 4$), Leber's congenital amaurosis ($n = 1$), congenital optical nerve atrophy ($n = 2$), and genetic defects that were not further specified ($n = 8$). All participants gave informed written consent and received course credit or monetary reimbursement for their participation. The study was ethically approved by the German Psychological Society (TB 122010) and conducted in accordance with the standards laid down in the Declaration of Helsinki.

Of twenty originally tested congenitally blind participants, one did not complete the experiment, and three were unable to discriminate between target and distractor stimuli. We recruited 45 sighted participants to establish a group of 16 control participants. We had developed and pre-tested the task in a young, sighted student population. We then tested the blind group before recruiting matched controls. For many older sighted participants, discriminating target and distractor stimuli proved too difficult. Accordingly, 23 sighted participants either decided to quit, or were not invited for the second experimental session because their performance in the first session had been at chance.

Moreover, technical failure during data acquisition prevented the use of data from two additional participants.

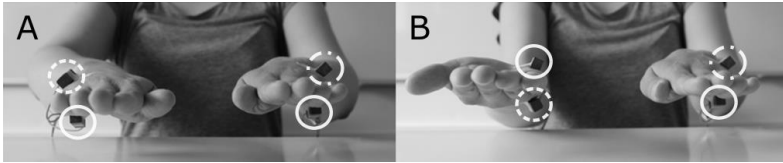


Figure 5.1. Experimental setup. Four vibro-tactile stimulators were attached to the palm and back of the hands (marked with white circles). The hands were either held in the same orientation with both palms facing downwards (**A**) or in different orientations with one hand flipped upside-down (**B**). In each trial, a target stimulus was randomly presented to one of the four locations. Simultaneously, a distractor stimulus was presented randomly at one of the stimulator locations on the other hand. Target and distractor stimuli differed with respect to their vibration pattern. Participants were asked to localize the target stimulus as quickly and accurately as possible. For statistical analysis and figures, stimulus pairs presented to the same anatomical locations were defined as congruent, as illustrated by dashed (target) and dashed-dotted (distractor) circles, which both point to the back of the hand here. Note that with differently oriented hands (**B**) anatomically congruent locations are incongruent in external space and vice versa.

5.2.2. Apparatus

Participants sat in a chair with a small lap table on their legs. They placed their hands in a parallel posture in front of them, with either both palms facing downwards (same orientation) or with one hand flipped upside down and the other facing downwards (different orientation). Whether the left or the right hand was flipped upside-down in the different orientation condition was counterbalanced across participants. Distance between index fingers of the hands was approximately 20 cm measured while holding both palms down. For reasons of comfort, and to avoid stimulators touching the table, the hands were supported by small foam cubes. Custom built vibro-tactile stimulators were attached to the back and to the palm of both hands midway between the root of the little finger and the wrist (Fig. 5.1). Participants wore earplugs and heard white noise via headphones to mask any auditory cues produced by the stimulators. Hand posture was monitored using a movement tracking system (Visualeyez II VZ4000v PTI; Phoenix Technologies Incorporated, Burnaby, Canada), with LED markers attached to the palm and back of the hands. The experiment was controlled using Presentation (version 16.2; Neurobehavioral Systems, Albany, CA, USA), which interfaced with Matlab (The Mathworks, Natick, MA, USA) and tracker control software VZSoft (Phoenix Technologies Incorporated, Burnaby, Canada).

5.2.3. Stimuli

The experiment comprised two kinds of tactile stimuli, namely, targets, to which participants had to respond, and distractors, which participants had to ignore. Target stimuli consisted of 200 Hz stimulation for 235 ms. Distractor stimuli had the same frequency, but included two gaps of 65 ms, resulting in three short bursts of 35ms each. To address our older sighted participants' difficulty with stimulus discrimination, we adjusted the distractor stimulus pattern for the last seven recruited control participants if they could not discriminate our original stimuli during a pre-experimental screening; such adjustments were made for three of these last seven participants, for the four other participants no adjustments were made.

In a first step, we increased the distractor's gap length to 75 ms, resulting in shorter bursts of 25 ms (1 participant). If the participant was still not able to discriminate between target and distractor, we set the distractor pattern to 50 ms "on", 100 ms "off", 5 ms "on", 45 ms "off",

and 35 ms “on” (2 participants). Note that, while these stimulus adjustments made discrimination easier, they did not affect the difficulty of the localization task. More importantly, they affected all experimental conditions equally. Yet, to ascertain that statistical results were not driven by these three control participants, we ran all analyses both with and without their data. The overall result pattern was unaffected, and we thus report results of the full control group.

5.2.4. Procedure

The experiment was divided into four large parts according to the combination of the two experimental factors Instruction (anatomical, external) and Movement Context (hands static, dynamic, that is, blockwise vs. frequent posture changes). The order of these four conditions was counterbalanced across participants. Participants completed both Movement Context conditions in a counterbalanced order, that is, the static and the dynamic part, under the first instruction within one session, and under the second instruction in a another session, which took part on another day. Participants completed four blocks of 48 trials for each combination of Instruction and Movement Context. Trials in which participants responded too fast ($RT < 100$ ms), or not at all, were repeated at the end of the block.

5.2.5. Manipulation of instruction

Under external instructions, participants reported whether the target stimulus was located “up” or “down” in external space and ignored the distractor stimulus. They had to respond as fast and accurately as possible by means of a foot pedal placed underneath one foot (left and right counterbalanced across participants). Participants responded by lifting the toes for target stimuli located “up” and by lifting the heel for target stimuli located “down”.

Under anatomical instructions, participants reported whether the target was presented to the palm or back of the hand by lifting the toes and the heel, respectively.

5.2.6. Manipulation of movement context

Under each set of instructions, participants performed the entire task once with a constant hand posture for entire experimental blocks (static condition), and once with hand posture varying from trial to trial (dynamic condition).

5.2.6.1. Static movement context

In the static context, posture was instructed verbally at the beginning of each block. A tone presented via loudspeakers signaled the beginning of a trial. After 1520 - 1700 ms (square distribution) a tactile target stimulus was presented randomly to one of the four locations. Simultaneously, a tactile distractor stimulus was presented to one of the two locations on the other hand. Hand posture was changed after completion of the second of four blocks. Start posture was counterbalanced across participants.

5.2.6.2. Dynamic movement context

In the dynamic context, an auditory cue at the beginning of each trial instructed participants either to retain (one beep, 1000 Hz sine, 100 ms) or to change (two beeps, 900 Hz sine, 100 ms each) the posture of the left or right hand (constant throughout the experiment, but counterbalanced across participants). After this cue onset, the trial continued only when the corresponding motion tracking markers attached to the hand surfaces had been continuously visible from above for 500 ms. If markers were not visible 5000 ms after cue onset, the trial was aborted and repeated at the end of the block. An error sound reminded the participant to adopt the correct posture. Tactile targets occurred equally often at each hand, so that targets and distractors, respectively, occurred half of the time on the moved, and half of the time on the unmoved, hand.

The order of trials, in which posture changed, and trials, in which posture remained unchanged, was pseudo-randomized in a way to assure equal amounts of trials for both conditions. This was done, for the entire experimental group, by drawing 10,000 samples from all possible trial orders; the number of trials in each condition was calculated for each permutation and permutations which contained the same number of trials for each condition were selected and an individual trial order was randomly assigned to each participant.

5.2.7. Practice

Before data acquisition, participants familiarized themselves with the stimuli by completing one block in which each trial contained only the target or the distractor, and participants reported which of the two had been presented. Next, participants localized 23 target stimuli without the presence of a distractor stimulus to practice the current task rules

(i.e., anatomical vs. external instructions). Finally, participants practiced five blocks of 18 regular trials, two with the hands in the same orientation, and three with the hands in different orientations. Auditory feedback was provided following incorrect responses during practice, but not during the subsequent experiment.

5.2.8. Data analysis

Data were analyzed and visualized in R (version 3.2.2; R Core Team, 2015) using the R packages lme4 (v1.1-9; Bates, Maechler, Bolker, & Walker, 2014), afex (v0.14.2; Singmann, Bolker, & Westfall, 2015), lsmeans (v2.20-2; Lenth & Hervé, 2015), dplyr (v0.4.3; Wickham & Francois, 2015), and ggplot2 (v1.0.1; Wickham, 2009). Trials with reaction times longer than 2000 ms were excluded from further analysis (5.58 % of all trials). Reaction times were analyzed for trials with correct responses only. It has been suggested that using an ANOVA to analyze categorical data is inappropriate (Jaeger, 2008). Therefore, we used generalized linear mixed models (GLMM) with a binomial link function to analyze accuracy (Bolker et al., 2009). We analyzed reaction times with linear mixed models (LMM).

To prevent that the fitted model's residuals violated normality and homoscedasticity assumptions, reaction times were box-cox transformed (Box & Cox, 1964) with $\lambda = -0.10$. Random intercepts and slopes per participants were estimated for each main effect; all reported (G)LMMs converged with this specification. Significance of fixed effects was assessed with likelihood ratio tests comparing the model with the maximal fixed effects structure and a reduced model without the fixed effect of interest (Pinheiro & Bates, 2000). These comparisons were calculated using the afex package (Singmann et al., 2015), and employed Type III sums of squares and sum-to-zero contrasts. Fixed effects were considered significant at $p < 0.05$. Post-hoc comparisons of significant interactions were conducted using approximate z-tests on the estimated least square means (LSM, lsmeans package; Lenth & Hervé, 2015). The resulting p-values were corrected for multiple comparisons following the procedure proposed by Holm (1979). To assess whether the overall result pattern differed between groups, we fitted a (G)LMM with the fixed between-subject factor Group (sighted, blind) and fixed within-subjects factors Instruction (anatomic, external), Posture (same, different), Congruency (congruent, incongruent), and Movement Context (static, dynamic). Congruency was

defined relative to anatomical locations for statistical analysis and figures. Subsequently, to reduce (G)LMM complexity and to ease interpretability, we conducted separate analyses for each participant group including the same within-subject fixed effects as before.

5.3. Results

We assessed how task instructions and movement context modulate the weighting of anatomically and externally coded spatial information in a tactile-spatial congruency task performed by sighted and congenitally blind individuals. Such weight changes should become evident in a modulation of congruency effects within hand postures that induce misalignment between these different reference frames. With differently oriented hands, stimulus pairs presented to anatomically congruent locations are incongruent in external space and vice versa, whereas the two coding schemes agree with the hands in the same orientation.

Thus, a modulation of reference frame weighting by task instructions would be evident in an interaction of Instruction, Posture, and Congruency. Furthermore, a modulation of weights by the movement context would be evident in an interaction of Movement Context, Posture, and Congruency. Accuracy and reaction times of sighted and congenitally blind groups are illustrated in Figure 5.2. A GLMM on accuracy (Table 5.2) with fixed effect factors Group, Instruction, Posture, Congruency, and Movement Context revealed a four-way interaction of Group, Instruction, Posture, and Congruency ($\chi^2(1) = 13.83$, $p < 0.001$) and a main effect of Movement Context ($\chi^2(1) = 4.54$, $p = 0.033$). Furthermore, there was a trend towards significance for the two-way interaction of Group and Movement Context ($\chi^2(1) = 3.47$, $p = 0.063$). An LMM of reaction times (Table 5.3) with fixed effects Group, Instruction, Posture, Congruency, and Movement Context revealed four-way interactions between Group, Instruction, Posture, and Congruency ($\chi^2(1) = 13.67$, $p < 0.001$) and between Group, Instruction, Posture, and Movement Context ($\chi^2(1) = 20.51$, $p < 0.001$).

Successively, we separately analyzed accuracy and reaction times for each group. We report results of the sighted group, followed by those of the blind group. For each group, we first present results for the task instruction manipulation, followed by those for the movement context manipulation.

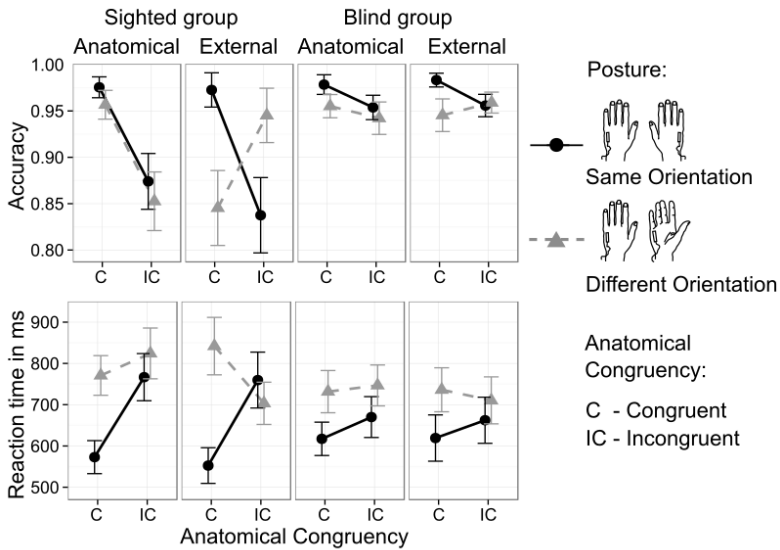


Figure 5.2. Performance in the tactile congruency task collapsed over static and dynamic movement conditions. Accuracy (top row) and reaction times (bottom row) are shown. Sighted (2 left columns) and congenitally blind participants (2 right columns) were instructed to localize tactile targets either relative to their anatomical (first and third column) or relative to their external spatial location (second and forth column). Hands were placed in the same (black circles) and in different orientations (grey triangles). Tactile distractors were presented to anatomically congruent (C) and incongruent (IC) locations of the other hand and had to be ignored. Congruency is defined in anatomical terms (see Fig. 5.1). Accordingly, with differently oriented hands, anatomically congruent stimulus pairs are incongruent in external space and vice versa. Whiskers represent the standard error of the mean. Although accuracy was analyzed with a log-link GLMM, we present untransformed percentage-correct values to allow a comparison to previous studies (see methods for details).

Table 5.2. Statistical results from accuracy analysis. Summary of the fixed effects in the GLMM of the sighted group, of the blind group, and of the combined analysis. Coefficients are logit units. Bold values indicate significance at $p < 0.05$. Italic values indicate a trend for significance at $p < 0.1$. Test statistics are χ^2 -distributed with 1 degree of freedom.

Predictor	Estimate	SE	χ^2	p
<i>Sighted group</i>				
(Intercept)	3.061	0.293		
Instruction	0.036	0.107	0.11	0.741
Posture	-0.137	0.064	3.46	0.063
Congruency	0.512	0.067	25.15	< .001
Context	0.049	0.075	0.44	0.507
Instruction X Posture	-0.011	0.043	0.06	0.808
Instruction X Congruency	0.306	0.043	49.48	< .001
Posture X Congruency	-0.482	0.043	138.31	< .001
Instruction X Context	0.046	0.043	1.12	0.290
Posture X Context	-0.052	0.042	1.50	0.221
Congruency X Context	0.057	0.042	1.76	0.184
Instruction X Posture X Congruency	0.391	0.042	81.43	< .001
Instruction X Posture X Context	0.002	0.042	0.00	0.953
Instruction X Congruency X Context	0.009	0.042	0.04	0.833
Posture X Congruency X Context	-0.028	0.042	0.45	0.500
Instruction X Posture X Congruency X Context	-0.04	0.042	0.88	0.347
<i>Blind group</i>				
(Intercept)	3.579	0.176		
Instruction	-0.031	0.117	0.07	0.794
Posture	-0.267	0.07	11.78	0.001
Congruency	0.179	0.068	5.61	0.018
Context	-0.153	0.07	3.92	0.048
Instruction X Posture	0.058	0.057	1.01	0.315
Instruction X Congruency	0.053	0.057	0.85	0.357
Posture X Congruency	-0.253	0.054	22.37	< .001
Instruction X Context	-0.041	0.056	0.50	0.479
Posture X Context	-0.029	0.054	0.28	0.598
Congruency X Context	0.012	0.054	0.05	0.823
Instruction X Posture X Congruency	0.131	0.053	6.00	0.014
Instruction X Posture X Context	-0.104	0.053	3.75	0.053
Instruction X Congruency X Context	0.027	0.053	0.25	0.620
Posture X Congruency X Context	0.033	0.053	0.37	0.544
Instruction X Posture X Congruency X Context	-0.043	0.053	0.63	0.427
<i>Both groups</i>				
(Intercept)	3.313	0.168		
Group	-0.282	0.168	2.69	0.101
Instruction	0.000	0.078	0.00	0.998
Posture	-0.211	0.038	20.48	< .001
Congruency	0.352	0.04	40.33	< .001
Context	-0.099	0.043	4.54	0.033
Group X Instruction	0.034	0.078	0.19	0.662
Group X Posture	0.046	0.039	1.43	0.232
Instruction X Posture	0.027	0.034	0.63	0.428
Group X Congruency	0.147	0.04	12.09	0.001
Instruction X Congruency	0.169	0.034	23.35	< .001
Posture X Congruency	-0.365	0.034	120.5	< .001
Group X Context	0.08	0.043	3.47	0.063
Instruction X Context	-0.004	0.034	0.02	0.901
Posture X Context	-0.038	0.034	1.20	0.273
Congruency X Context	0.035	0.034	1.06	0.304
Group X Instruction X Posture	-0.047	0.034	1.85	0.174
Group X Instruction X Congruency	0.145	0.034	17.57	< .001
Group X Posture X Congruency	-0.113	0.034	10.75	0.001
Instruction X Posture X Congruency	0.26	0.034	58.31	< .001
Group X Instruction X Context	0.044	0.034	1.64	0.201
Group X Posture X Context	-0.022	0.034	0.42	0.519
Instruction X Posture X Context	-0.051	0.034	2.20	0.138
Group X Congruency X Context	0.023	0.034	0.47	0.493
Instruction X Congruency X Context	0.018	0.034	0.27	0.605
Posture X Congruency X Context	0.004	0.034	0.01	0.915
Group X Instruction X Posture X Congruency	0.129	0.034	13.83	< .001
Group X Instruction X Posture X Context	0.054	0.034	2.46	0.117
Group X Instruction X Congruency X Context	-0.01	0.034	0.09	0.766
Group X Posture X Congruency X Context	-0.03	0.034	0.77	0.380
Instruction X Posture X Congruency X Context	-0.043	0.034	1.62	0.203
Group X Instruction X Posture X Congruency X Context	0.000	0.034	0.00	0.993

Table 5.3. Statistical results from reaction time analysis. Summary of the fixed effects in the LMM of the sighted group, of the blind group, and of the combined analysis. Coefficients were derived after Box-Cox transformation. Bold values indicate significance at $p < 0.05$. Italic values indicate a trend for significance at $p < 0.1$. Test statistics are χ^2 - distributed with 1 degree of freedom.

Predictor	Estimate	SE	χ^2	p
<i>Sighted group</i>				
(Intercept)	5.327	0.046		
Instruction	0.017	0.014	1.34	0.247
Posture	0.058	0.005	33.84	< .001
Congruency	-0.033	0.007	14.39	< .001
Context	0.029	0.009	7.60	0.006
Instruction X Posture	0.003	0.002	1.58	0.209
Instruction X Congruency	-0.016	0.002	50.23	< .001
Posture X Congruency	0.049	0.002	447.97	< .001
Instruction X Context	0.004	0.002	2.77	0.096
Posture X Context	0.000	0.002	0.04	0.834
Congruency X Context	0.003	0.002	1.56	0.212
Instruction X Posture X Congruency	-0.017	0.002	52.98	< .001
Instruction X Posture X Context	-0.004	0.002	3.49	0.062
Instruction X Congruency X Context	0.001	0.002	0.32	0.574
Posture X Congruency X Context	-0.001	0.002	0.28	0.598
Instruction X Posture X Congruency X Context	0.002	0.002	0.74	0.389
<i>Blind group</i>				
(Intercept)	5.316	0.042		
Instruction	0.006	0.015	0.17	0.678
Posture	0.049	0.006	26.58	< .001
Congruency	-0.011	0.004	5.17	0.023
Context	0.027	0.01	5.50	0.019
Instruction X Posture	-0.001	0.002	0.54	0.462
Instruction X Congruency	-0.006	0.002	8.63	0.003
Posture X Congruency	0.013	0.002	44.35	< .001
Instruction X Context	-0.005	0.002	7.47	0.006
Posture X Context	-0.013	0.002	43.44	< .001
Congruency X Context	0.008	0.002	17.92	< .001
Instruction X Posture X Congruency	-0.005	0.002	7.26	0.007
Instruction X Posture X Context	0.009	0.002	22.23	< .001
Instruction X Congruency X Context	0.001	0.002	0.12	0.724
Posture X Congruency X Context	-0.001	0.002	0.22	0.641
Instruction X Posture X Congruency X Context	0.000	0.002	0.05	0.830
<i>Both groups</i>				
(Intercept)	5.321	0.031		
Group	0.006	0.031	0.03	0.852
Instruction	0.012	0.01	1.24	0.265
Posture	0.054	0.004	60.45	< .001
Congruency	-0.022	0.004	20.76	< .001
Context	0.028	0.007	12.88	< .001
Group X Instruction	0.005	0.01	0.28	0.594
Group X Posture	0.004	0.004	1.13	0.287
Instruction X Posture	0.001	0.002	0.20	0.658
Group X Congruency	-0.011	0.004	6.71	0.010
Instruction X Congruency	-0.011	0.002	53.05	< .001
Posture X Congruency	0.031	0.002	417.83	< .001
Group X Context	0.001	0.007	0.03	0.868
Instruction X Context	-0.001	0.002	0.30	0.581
Posture X Context	-0.007	0.002	20.52	< .001
Congruency X Context	0.006	0.002	14.08	< .001
Group X Instruction X Posture	0.002	0.002	1.95	0.162
Group X Instruction X Congruency	-0.005	0.002	11.45	0.001
Group X Posture X Congruency	0.018	0.002	136.92	< .001
Instruction X Posture X Congruency	-0.011	0.002	52.72	< .001
Group X Instruction X Context	0.005	0.002	9.47	0.002
Group X Posture X Context	0.006	0.002	17.73	< .001
Instruction X Posture X Context	0.003	0.002	2.93	0.087
Group X Congruency X Context	-0.003	0.002	3.49	0.062
Instruction X Congruency X Context	0.001	0.002	0.43	0.513
Posture X Congruency X Context	-0.001	0.002	0.50	0.479
Group X Instruction X Posture X Congruency	-0.006	0.002	13.67	< .001
Group X Instruction X Posture X Context	-0.007	0.002	20.51	< .001
Group X Instruction X Congruency X Context	0.000	0.002	0.04	0.849
Group X Posture X Congruency X Context	0.000	0.002	0.01	0.927
Instruction X Posture X Congruency X Context	0.001	0.002	0.25	0.618
Group X Instruction X Posture X Congruency X Context	0.001	0.002	0.59	0.444

5.3.1. Sighted group: Manipulation of task instruction

Accuracy

The GLMM for the sighted group (Table 5.2) revealed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 81.43$, $p < 0.001$), suggesting that congruency effects differed in dependence of Instruction. Indeed, post-hoc comparisons revealed a two-way interaction between Posture and Congruency under external ($z = 14.80$, $p < 0.001$), but not under anatomical instructions ($z = 1.50$, $p = 0.133$).

When the hands were in the same orientation, congruency matched for anatomical and external reference frames, and participants responded more accurately following (anatomically and externally) congruent than incongruent stimulation (Fig. 5.2, 1st and 2nd column, top, black circles). This effect was present for anatomical ($z = 8.36$, $p < 0.001$) and external instructions ($z = 10.26$, $p < 0.001$). When the hands were oriented differently (Fig. 5.2, gray triangles), stimulus pairs were always congruent anatomically when they were incongruent externally, and vice versa. An anatomical congruency effect was present under anatomical instructions ($z = 7.87$, $p < 0.001$). Importantly, the congruency effect was reversed under external instructions, with more correct performance for externally congruent stimulus pairs ($z = -7.32$, $p < 0.001$). Thus, the direction of the tactile congruency effect depended on the instructions.

Reaction times

The pattern of sighted participants' reaction times was qualitatively similar to that of the accuracy results. The LMM (Table 5.3) showed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 52.98$, $p < 0.001$), indicating that instructions affected the congruency effect. Post-hoc comparisons yielded a two-way interaction between Posture and Congruency under anatomical ($z = 9.99$, $p < 0.001$) and external instructions ($z = 20.25$, $p < 0.001$). With both hands in the same orientation (Fig. 5.2, black circles), sighted participants responded faster to (anatomically and externally) congruent stimulus pairs than to incongruent stimulus pairs, regardless of instruction (external instruction: $z = 10.47$, $p < 0.001$; anatomical: $z = 10.37$, $p < 0.001$).

With differently oriented hands (Fig. 5.2, gray triangles), an anatomical, yet smaller than in the same orientation conditions, congruency effect emerged under anatomical instructions ($z = 2.14$, $p = 0.034$) and an

externally coded congruency effect emerged under external instructions ($z = -6.23$, $p < 0.001$).

In sum, analysis of accuracy and reaction times consistently reflected performance modulations that were consistent with the instructed spatial coding – anatomical or external – in sighted participants.

5.3.2 Sighted group: Manipulation of movement context

Accuracy

In contrast to the effects of task instructions, neither the effect of Movement Context (see Fig. 5.3 left, Fig. 5.4 top) nor the interactions of Movement Context and any other variable were significant in the GLMM on accuracy (all $\chi^2(1) \leq 1.50$, $p \geq 0.221$). To demonstrate that these null effects were not due simply to high variance or a few outliers, Fig. 5.4 illustrates individual participants' performance.

Reaction times

For reaction times, the LMM revealed a main effect of Movement Context ($\chi^2(1) = 7.60$, $p = 0.005$), indicating that sighted participants responded overall faster in the static than in the dynamic movement context. In addition, there was a trend for a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 3.49$, $p = 0.062$), due to a larger reaction time gain under anatomical than under external instructions, but only when the hands were in the same orientation: in this latter case, the two-way interaction of Instruction and Movement Context was significant ($z = 2.51$, $p = 0.024$); participants responded faster in the static than in the dynamic condition under anatomical instructions ($z = 3.72$, $p = 0.008$), and this effect was reduced under external instructions ($z = 2.12$, $p = 0.034$). With the hands in different orientations, the two-way interaction between Instruction and Movement was not significant ($z = -0.14$, $p = 0.886$). Thus, an effect of movement was evident in all conditions, though the marginal three-way interaction of Instruction, Posture, and Movement Context suggested that its extent was different across conditions.

In sum, although frequent movement generally slowed reaction times, movement context did not affect the congruency effect in either of the present study's dependent measures, accuracy or reaction times.

5.3.3. Congenitally blind group: Manipulation of task context

Accuracy

The GLMM on blind participants' accuracy revealed a significant three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 6.00$, $p = 0.014$), suggesting that task instructions modulated the congruency effect. Post-hoc comparisons revealed a two-way interaction between Posture and Congruency under external instructions ($z = 4.91$, $p < 0.001$) and a trend for a two-way interaction under anatomical instructions ($z = 1.66$, $p = 0.097$).

With hands in the same orientation, participants responded more accurately following (anatomically and externally) congruent than incongruent stimulation (Fig. 5.2, 3rd and 4th column, top, black circles), regardless of whether they were instructed anatomically ($z = 2.92$, $p = 0.011$) or externally ($z = 3.75$, $p = 0.001$).

With differently oriented hands (Fig. 5.2, 3rd and 4th column, top, gray triangles), performance was not significantly affected by congruency under anatomical instructions ($z = 1.06$, $p = 0.290$). In contrast, under external instructions, the effect of congruency showed a reversed pattern as with hands in the same orientation, with more accurate responses when stimulus pairs were externally congruent (but anatomically incongruent) than when they were externally incongruent (but anatomically congruent, $z = -2.56$, $p = 0.021$).

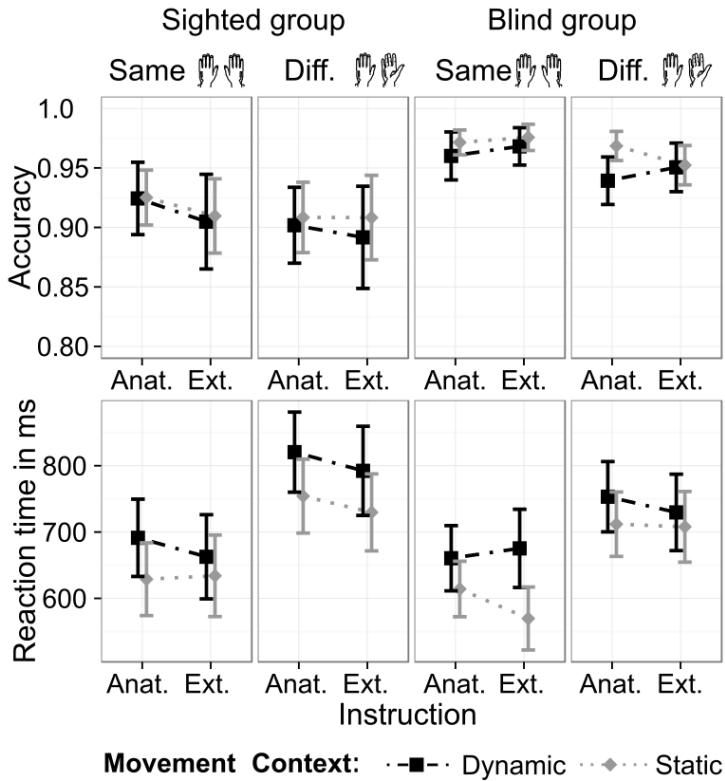


Figure 5.3. Effect of Movement Context on accuracy and reaction times, collapsed over congruency conditions. Participants localized tactile targets with hands in the same (first and third column) and in different orientations (second and fourth column), under anatomical (“Anat.”) and under external instructions (“Ext.”), in the context of static blockwise posture changes (gray diamonds) and in the context of frequent trial-by-trial posture changes (black squares). Error bars show standard errors of the mean.

Reaction times

Reaction time analysis corroborated accuracy results. The LMM on blind participants' reaction times revealed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 7.26, p = 0.007$; see Fig. 5.2, 3rd and 4th column, bottom). Post-hoc comparisons revealed a two-way interaction between Posture and Congruency under anatomical ($z = 2.79, p = 0.005$) and external instructions ($z = 6.65, p < 0.001$).

With hands held in the same orientation, blind participants responded significantly faster to (anatomically and externally) congruent than incongruent stimulus pairs under anatomical ($z = 4.41, p < 0.001$) and under external instructions ($z = 4.26, p < 0.001$).

With differently oriented hands, no significant congruency effect was observed under anatomical instructions ($z = 1.55, p = 0.120$). The congruency effect was reversed under external instructions relative to the congruency effect when the hands were held in the same orientation, with faster responses to externally congruent (but anatomically incongruent) than externally incongruent (but anatomically congruent) stimulus pairs ($z = -2.48, p = 0.026$).

In sum, both accuracy and reaction times of blind participants reflected an influence of task instructions on tactile-spatial congruency coding.

5.3.4 Congenitally blind group: Manipulation of movement context

Accuracy

The GLMM on blind participants' accuracy showed a main effect of Movement Context (Fig. 5.3, 3rd and 4th column; $\chi^2(1) = 3.92, p = 0.048$), with more accurate responses in the static than in the dynamic context. Moreover, there was a trend for a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 3.75, p = 0.053$). Following up on this trend, post-hoc comparisons yielded a trend for a two-way interaction between Instruction and Movement Context with hands in different orientations ($z = -2.15, p = 0.063$), but not with hands in the same orientation ($z = 0.73, p = 0.465$).

Following up on the two-way interaction between Instruction by Movement Context revealed that static and dynamic conditions did not significantly differ under either instruction when the hands were in the same orientation, (anatomical: $z = 0.50, p = 0.618$; external: $z = 1.36, p = 0.173$). With differently oriented hands, participants responded more accurately in the static than in the dynamic condition under anatomical ($z = 3.09, p = 0.004$), but not under external instructions ($z = 0.37, p =$

0.713). Thus, the performance pattern was suggestive of some selective effects of task instructions on accuracy, but the statistical results were only marginal.

We had hypothesized that frequent posture changes would emphasize the weighting of external spatial information. Such an effect would be evident in a modulation of congruency effects emerging with hands in different postures. The corresponding interaction in the GLMM was not significant, that is, a four-way interaction of Instruction, Posture, Congruency, and Movement Context ($\chi^2(1) = 0.63, p = 0.427$). Yet, visual inspection of Fig. 5.4 suggested that an effect may be present, but remained non-significant due to lack of power of a GLMM with several factors. Therefore, we performed hypothesis-based post-hoc tests for conditions with differently oriented hands. In the static condition, no significant congruency effect was present under anatomical instructions ($z = 0.52, p = 0.605$), but a trend for a congruency effect was observed under external instructions ($z = -2.34, p = 0.078$). In the dynamic condition, no significant congruency effect was present under anatomical instructions ($z = 1.15, p = 0.252$) and external instructions ($z = -1.48, p = 0.138$). Thus, even when directly comparing movement conditions while ignoring other experimental conditions, the hypothesis that movement modulates spatial integration in tactile congruency coding of congenitally blind humans did not receive any substantial support.

Reaction times

The LMM on reaction times revealed a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 22.23, p < 0.001$), suggesting a modulation of the congruency effect on reaction times by Movement Context.

Following up on the three-way interaction, post-hoc comparisons yielded a two-way interaction between Instruction and Movement Context with hands in the same ($z = -5.30, p < 0.001$), but not in different orientations ($z = 1.39, p = 0.163$).

Blind participants responded significantly faster in the static than in the dynamic condition with hands in the same orientation under external instructions ($z = 5.01, p < 0.001$), but only marginally faster under anatomical instructions ($z = 2.27, p = 0.069$). No significant difference between conditions was observed with differently oriented hands under either instruction (anatomical: $z = 1.58, p = 0.113$; external: $z = 0.85, p = 0.391$).

An influence of frequent posture changes on the weighting of external spatial information should be evident in a modulation of congruency effects with the hands oriented differently rather than in the same posture. Just like for accuracy, the corresponding four-way interaction of Instruction, Posture, Congruency, and Movement Context was not significant for reaction times ($\chi^2(1) = 0.05, p = 0.830$). Although there was a two-way interaction of Congruency and Movement Context ($\chi^2(1) = 17.92, p < 0.001$) with a congruency effect in the static ($z = 4.02, p < 0.001$), but not than in the dynamic condition ($z = 0.47, p = 0.635$), this interaction does not differentiate between instructions and postures. As had been the case with accuracy, visual inspection of the reaction times result pattern (Fig. 5.5, bottom) suggested – as hypothesized – posture may have modulated the congruency effect in the expected direction, but a lack of power may have prevented statistical significance. Therefore, we conducted hypothesis-driven post-hoc tests of the relevant conditions (i.e., conditions with differently oriented hands). Under anatomical instructions, a congruency effect was present in the static movement context ($z = 2.06, p = 0.047$), but not in the dynamic movement context ($z = 0.13, p = 0.900$). Under external instructions, a significant congruency effect was not evident in the static ($z = -0.96, p = 0.335$), but in the dynamic context ($z = -3.06, p = 0.009$), with faster responses for externally congruent (but anatomically incongruent) than externally incongruent (but anatomically congruent) stimulus pairs. These comparisons imply that an anatomical congruency effect was present under anatomical instructions only in the static context and an external congruency effect under external instruction only in the dynamic context. While the presence of these partial instruction-related effects is in line with our hypotheses, the lack of a significant higher-order interaction precludes any strong interpretation of these direct statistical tests. Specifically, congruency effects decreased numerically in all instruction and posture conditions (see Fig. 5.5, bottom), an effect that does not comply with our hypothesis about an effect of the movement context. Furthermore, congruency effects appeared to be quite variable across blind participants, as evident in individual modulations of congruency effects (see Fig. 5.5), further corroborating the conclusion that reliable modulations of congruency by movement context were not present on the group level.

5.3.5. Comparison of the congruency effect between sighted and congenitally blind participants

Visual inspection of Figure 5.2 suggests that congruency effects on accuracy and on reaction times were overall larger in the sighted than in the blind group. For accuracy, this difference seems to stem from the blind participants outperforming sighted participants when responding to stimulus pairs that were incongruent relative to the instructed reference frame (i.e., anatomically incongruent under anatomical instructions and externally incongruent under external instructions). For statistical testing, we accordingly followed up on the significant four-way interaction between Group, Instruction, Posture, and Congruency for both accuracy and reaction times (see Tables 5.2 and 5.3) with post-hoc comparisons for each combination of Instruction and Posture. Indeed, there were significant two-way interactions between Group and Congruency, with larger congruency effects in the sighted than in the blind group for almost all combinations of Instruction and Posture for both accuracy and reaction times (Table 5.4A, bold font).

Moreover, blind participants responded more accurately than sighted participants following stimulus pairs that were anatomically incongruent under anatomical instructions and externally incongruent under external instructions (all $p \leq 0.016$, bold font in Table 5.4B). These advantages for the blind group were evident only in accuracy, but not in reaction times (all $p \geq 0.296$; Table 5.4B).

Table 3. A, Interaction between Group and Congruency for each instruction and posture

	anatomical instruction		external instruction	
	same posture	different posture	same posture	different posture
Accuracy	$z = 3.65,$ $p < 0.001$	$z = 4.81,$ $p < 0.001$	$z = 2.99,$ $p = 0.003$	$z = -3.88,$ $p < 0.001$
Reaction times	$z = -5.89,$ $p < 0.001$	$z = -0.82,$ $p = 0.412$	$z = -6.10,$ $p < 0.001$	$z = 3.65,$ $p < 0.001$

B, Comparison between groups for each combination of Instruction, Posture, and Congruency

Accuracy				
	anatomical instruction		external instruction	
	same posture	different posture	same posture	different posture
Congruent	$z = -0.13,$ $p = 0.895$	$z = -0.29,$ $p = 0.774$	$z = 0.73,$ $p = 0.465$	$z = 2.40,$ $p = 0.016$
Incongruent	$z = 2.67,$ $p = 0.008$	$z = 2.85,$ $p = 0.004$	$z = 3.35,$ $p < 0.001$	$z = -0.09,$ $p = 0.932$
Reaction times				
Congruent	$z = 0.75,$ $p = 0.454$	$z = -0.47,$ $p = 0.641$	$z = 0.86,$ $p = 0.385$	$z = -0.58,$ $p = 0.564$
Incongruent	$z = -1.05,$ $p = 0.296$	$z = -0.71,$ $p = 0.475$	$z = -0.74,$ $p = 0.459$	$z = 0.42,$ $p = 0.678$

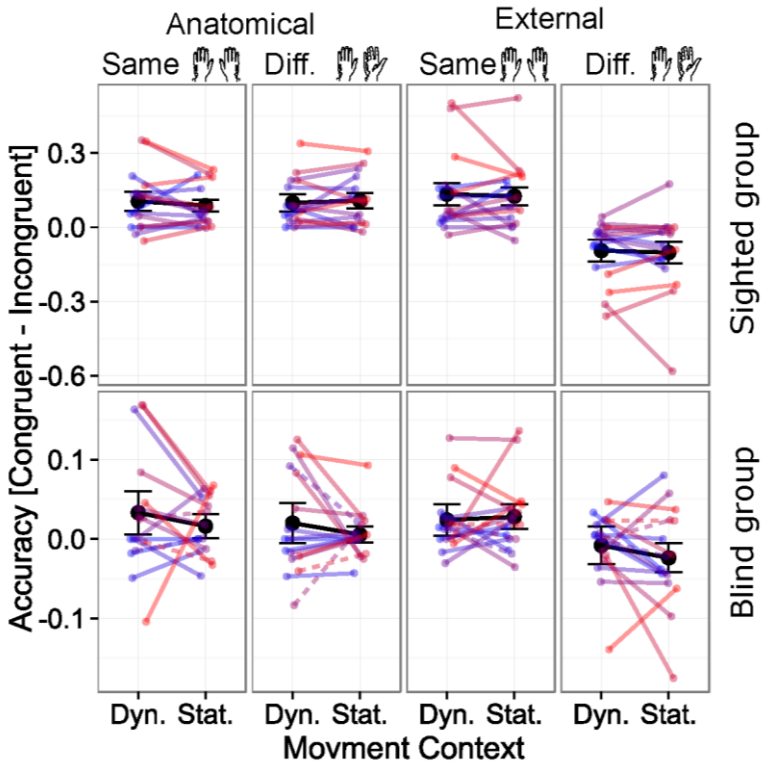


Figure 5.4. Individual participants' tactile congruency effects in accuracy. Responses from anatomically incongruent trials were subtracted from responses in congruent trials. Congruency effects are plotted for dynamic ("Dyn.") and static ("Stat.") contexts with hands in the same (1st and 3rd column) and in different orientations (2nd and 4th column) under anatomical (1st and 2nd column) and external instructions (3rd and 4th column) in the sighted (top row) and in the congenitally blind group (bottom row). Note that scales differ between groups because effects in the blind group were much smaller than in the sighted group. Mean congruency effects for each condition are plotted in black, whiskers represent SEM. Each color represents one participant.

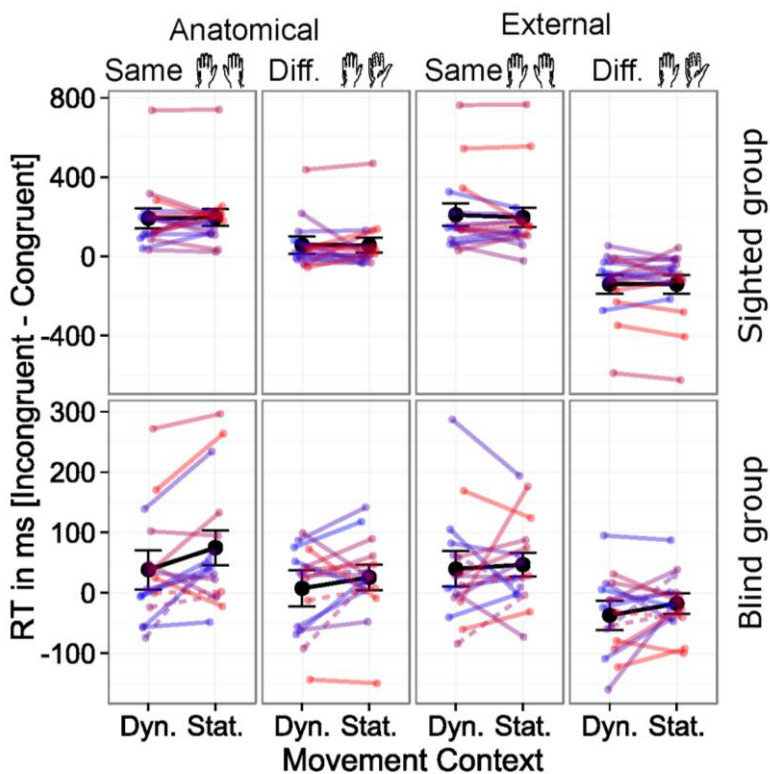


Figure 5.5. Individual participants' tactile congruency effects in reaction times. Responses from anatomically incongruent trials were subtracted from responses in congruent trials. Congruency effects are plotted for dynamic ("Dyn.") and static ("Stat.") contexts with hands in the same (1st and 3rd column) and in different orientations (2nd and 4th column) under anatomical (1st and 2nd column) and external instructions (3rd and 4th column) in the sighted (top row) and in the congenitally blind group (bottom row). Note that scales differ between groups because effects in the blind group were much smaller than in the sighted group. Mean congruency effects for each condition are plotted in black, whiskers represent SEM. Each color represents one participant.

5.4. Discussion

The present study investigated whether congenitally blind humans integrate anatomical and external spatial information during tactile localization in a flexible manner similarly to sighted humans. By manipulating hand posture, we varied the congruency of target and distractor locations relative to both anatomical and external spatial reference frames. The study comprised two contextual manipulations, both of which have been demonstrated to influence tactile localization performance in sighted humans. First, we manipulated task context by formulating task instructions with reference to anatomical vs. external spatial terms (hand surfaces vs. elevation in space). Second, we manipulated movement context by asking participants to leave the hands in the same posture for entire experimental blocks, or to change hand posture in a trial-by-trial fashion.

With the hands in the same posture, both sighted and congenitally blind participants responded faster and more accurately to (anatomically and externally) congruent than incongruent target-distractor pairs. With differently oriented hands, task instruction modulated the size and direction of congruency effects. Specifically, under anatomical instructions, sighted participants responded faster and more accurately to anatomically congruent than anatomically incongruent target-distractor pairs, whereas blind participants did not exhibit a significant congruency effect, but instead responded similarly to congruent and incongruent target-distractor pairs. In contrast, under external instructions, both sighted and congenitally blind participants responded faster and more accurately to externally congruent (but anatomically incongruent) than externally incongruent target-distractor pairs, even if these effects were smaller in blind participants. Movement context, that is, static hand positioning versus frequent posture change, did not significantly modulate congruency effects.

5.4.1. Flexible weighting of reference frames in both sighted and blind individuals

Auditory information coded in an external spatial reference frame is available to both sighted and congenitally blind individuals (Röder et al., 2007). Yet, tactile external spatial information has long been presumed to be automatically integrated only by normally sighted and late blind, but not by congenitally blind individuals, suggesting that visual experience during ontogeny plays a critical role in tactile-spatial coding

(Collignon et al., 2009; Röder et al., 2008, 2004). In the present study, blind participants' performance should have been independent of posture and instructions if they had relied on anatomical information alone. In contrast to this assumption, blind participants' congruency effects were coded in an external reference frame when the task had been instructed externally. Moreover, under anatomical instructions, a congruency effect emerged only when the hands were in the same orientation.

The flexible and strategic weighting of anatomical and external tactile information, observed here in both sighted and blind individuals, presumably reflects top-down regulation of spatial integration. In line with this proposal, anatomical and external spatial information are presumed to be available concurrently, as evident, for instance, in event-related potentials (Heed & Röder, 2010) and in oscillatory brain activity (Buchholz et al., 2011, 2013; Schubert et al., 2015). Furthermore, performance under reference frame conflict, for instance due to hand crossing, is modulated by a secondary task, and this modulation reflects stronger weighting of external information when the secondary task accentuates an external as compared to anatomical spatial code (Badde, Röder, et al., 2015). The present results, too, demonstrate directed, top-down mediated modulations of spatial weighting, with anatomical task instructions biasing weighting towards anatomical coding, and external instructions biasing weighting towards external coding.

5.4.2 Comparison with previous tactile localization studies in blind individuals

The effect of hand posture on tactile localization for congenitally blind participants in the present study contrasts with findings from previous studies. In several experiments, blind participants' performance did not differ between hand postures, and these results have been interpreted as indicating that congenitally blind individuals do not use external spatial information by default for tactile localization (Collignon et al., 2009; Röder et al., 2008, 2004). Several aspects of the present study may account for the differences we observed compared to previous reports. First, most previous studies have manipulated the congruence of anatomical and external spatial information by means of hand crossing. In contrast, here posture was modulated by manipulating the up-down orientation of the hands. Thus, each hand remained in its

hemispace. Turning the hands upside down changes the gravitational pull on the hands between conditions. In addition, different parts of the hand (palm vs. back of the hand) rested on the table in different posture conditions, and, thus, may have provided additional external-spatial information in the vertical direction. Second, distractor interference on tactile localization in the present study may have operated on a different processing level compared to previous studies, which ask for tactile localization without any distractors being present (Collignon et al., 2009; Röder et al., 2008, 2004). Third, the context of the task may have emphasized the weighting of external spatial information in the blind group in comparison to previous studies. The present response with a foot pedal requires a spatial mapping of the target location to the location of the foot that had to be lifted. Such a spatial mapping was not required in previous studies (Röder et al., 2008, 2004). Additionally, the sequence of conditions in the present study may have played a role. Blind participants who started in the static context under anatomical instructions ($n = 3$; Fig. 5.4 & 5.5, dashed lines) did not appear to show a modulation of congruency effects by hand posture. Yet, this could not be confirmed in an exploratory analysis due to lack of power.

In sum, congruency effects in the blind group changed with task instructions in a similar manner as in the sighted group; this finding suggests that flexible and strategic weighting of anatomical and external spatial information emerges even in the absence of vision from birth.

5.4.3 Comparison of sighted participants' susceptibility to task instruction with previous studies

A previous study employed a similar tactile congruency task as that of the present study, though only within sighted individuals: This study reported that the congruency effect always depended on the external spatial location of tactile stimuli, independent of task instructions (Gallace et al., 2008). These previous results are at odds with the present finding of performance biases that depended on the reference frame used in the task instructions. Gallace and colleagues (2008) attributed their results to the spatial stimulus-response mapping their study employed: target locations were assigned to different response locations (i.e., lifting the toes versus lifting the heel) (Gallace et al., 2008). Possibly response mapping to the footpedal set such a strong external context, that an influence of anatomical instructions could not show. Indeed, with verbal responses the congruency effect depended

on the reference frame implied by the instruction, similarly as we report here, despite of the use of foot pedals as response devices (Gallace et al., 2008). The observed differences between the present and the study by Gallace and colleagues may be explained by at least three factors. First, Gallace and colleagues (2008) presented stimuli to the tips of the index fingers and the thumbs while participants held two foam cubes. Because the to-be-grasped object needs to be encoded within the external world, the involvement of these external objects could have induced a greater weighting of external information in the previous study by Gallace and colleagues. Second, the spatial relations between two points on the palm and back of the hand, such as their absolute distance, are fixed, whereas such spatial relationships vary for the fingers. The involvement of body parts that can flexibly change their relative location may contribute, thus, to an overall stronger weighting of an external reference frame. Third, non-informative vision (Newport et al., 2002) as well as online visual information about the crossed posture of artificial rubber hands (Azañón & Soto-Faraco, 2007) seem to evoke an emphasis of the external reference frame. Online visual information (Cadieux & Shore, 2013; Gallace et al., 2008) about the current hand posture may, thus, have led to the dominance of the external congruency effect. In contrast, in our study sighted participants were blindfolded for comparability with blind participants, so that no visual information was available during the experiment, potentially biasing weighting away from external spatial coding.

5.4.4. Weak evidence for an effect of movement context in blind, but not in sighted participants

Based on previous findings with other tactile localization paradigms that manipulated movement (Azañón et al., 2015; Heed, Möller, et al., 2015; Hermosillo et al., 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012), we had expected that frequent posture change would emphasize the weighting of an external reference frame in both sighted and blind participants. Sighted participants responded faster overall in the static than in the dynamic context. However, this effect did not significantly differ across postures, instructions, and congruency conditions and, thus, appears to have been related to increased task difficulty rather than to differential weighting of spatial reference frames. The reason for the lack of a movement context effect in the present study is unclear; it may be related to the specific localization paradigm employed here, as

previous reports of movement-related performance modulation were based on a hand-crossing paradigm (Azañón et al., 2015; Heed, Möller, et al., 2015; Hermosillo et al., 2011).

It may strike as surprising that a movement context effect was marginally significant in the blind participant group, but not in the sighted group. Yet, stronger reliance of blind than sighted participants on external spatial coding is not unprecedented; in a bimanual coordination task that involved both anatomical and external spatial reference frames, congenitally blind participants appeared to rely entirely on external coding, whereas sighted participants appeared to use both anatomical and external coding (Heed & Röder, 2014). However, firm interpretation of this possible difference between sighted and blind participants must await confirmation through replication.

5.4.5. Enhanced vibrotactile discrimination in congenitally blind individuals

Congenitally blind performed more accurately compared to sighted participants when target and distractor were anatomically incongruent under anatomical instructions and externally congruent under external instructions. In addition, many sighted participants had to be excluded because they had been unable to discriminate the original distractor from the target stimulus, whereas only few blind participants had this problem. These findings suggest that blind participants had a general advantage over sighted participants in the dissociation between vibrotactile patterns. Indeed, congenitally blind participants reportedly discriminate vibrotactile stimuli better than sighted participants when the vibration frequency ranges from 20 to 100 Hz (Wan, Wood, Reutens, & Wilson, 2010). Tactile target and distractor stimuli of the present experiment differed at an even lower frequency, with the distractors' timing pulsed at 10 Hz. This finding, thus, adds to the notion of enhanced frequency discrimination of congenitally blind individuals at low vibrotactile frequencies (Wan et al., 2010).

5.4.6. Summary and conclusion

In sum, we have reported that both sighted and congenitally blind individuals can flexibly adapt the weighting of anatomical and external information during the encoding of touch, evident in the dependency of tactile congruency effects on task context. However, of two tested

context manipulations, namely task instructions and movement, only the former evoked reliable modulations of tactile localization behavior. Although the movement context led to slowed responses in sighted individuals, this modulation was unrelated to the weighting of spatial information. Moreover, visually apparent evidence for an effect of the movement context on the weighting of spatial information in the blind group was statistically unreliable, precluding firm conclusions about the movement manipulation for this group. In contrast, the present study revealed strong effects of task instructions on reference frame weighting not just in sighted, but also in congenitally blind individuals. These results demonstrate that congenitally blind individuals do not rely on only a single reference frame but, instead, flexibly integrate anatomical and external spatial information, indicating that spatial integration in touch does not ultimately depend on the availability of vision during development.

**Chapter 6:
Influences of movement planning
on tactile perception**

Introduction

The brain is constantly exposed to signals coming from multiple senses. Remarkably, the brain is able to construct a coherent percept from these signals in order to successfully interact with objects in the surrounding space. Spatial information is initially represented in a modality specific manner: Visual information is represented in a retinotopic, eye-centered reference frame, auditory information relative to the head, and tactile information in an anatomical, skin-based reference frame. In the tactile modality such a representation is reflected in the homuncular organization of the primary somatosensory cortex (Penfield & Boldrey, 1937). Tactile stimuli are thought to be remapped from an anatomical reference frame into an external reference frame, even when task demands would not require a remapping (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). It is thought that the brain constantly remaps sensory information coming from different senses into a common external, possibly eye-centered, representation to facilitate integration with other modalities (Pouget, Ducom, et al., 2002). In touch, both anatomical and the remapped external spatial information are thought to be flexibly weighted and integrated and, thus, to be encoded concurrently (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015; Heed, Buchholz, et al., 2015). The remapping of tactile information, thus, appears to facilitate integration with information of other modalities. Therefore, together with information from other senses, a location estimate of a tactile event in the environment may be derived. Estimating the location of an external tactile or multisensory event is necessary to act towards the event with a motor response. Motor responses in the saccadic system have been associated with shifts of attention as formulated in the premotor theory of attention (Rizzolatti et al., 1987, 1994). For instance, saccadic eye movements and covert attention activate largely overlapping brain areas (Corbetta, 1998; Nobre, Gitelman, Dias, & Mesulam, 2000). The premotor theory of attention claims that processing is enhanced at the goal of a movement (Rizzolatti et al., 1994).

In line with this claim visual, auditory, and tactile discrimination performance is enhanced at the saccadic endpoint prior to saccade onset compared to non-endpoint locations (Deubel & Schneider, 1996; Juravle & Deubel, 2009; Rorden & Driver, 1999; Rorden et al., 2002). In

addition, visual, auditory, and somatosensory ERP amplitudes are enhanced when stimulus location coincides with the subsequent saccadic movement goal (Collins et al., 2010; Eimer et al., 2006; Gherri et al., 2008; Gherri & Eimer, 2008). These enhancements related to saccade planning have been observed in time ranges that are also sensitive to covert shifts of attention: For instance, both covert tactile attention and saccadic movement planning have been reported to enhance somatosensory ERPs in the time range of the N140, when comparing activity following tactile stimuli at the covertly attended versus the unattended hand, and when comparing activity following tactile stimuli at the saccade goal versus non-saccade goal (Gherri & Eimer, 2008). The premotor theory of attention was soon extended to include not only the saccadic system but also manual movements: Visual performance has been shown to be enhanced at the motor endpoints of manual reaching and grasping movements (Baldauf, Wolf, & Deubel, 2006; Collins, Schicke, & Röder, 2008; Deubel & Schneider, 2004; Deubel, Schneider, & Paprotta, 1998; Schiegg, Deubel, & Schneider, 2003). Similarly, planning a finger lift has been reported to enhance somatosensory ERPs in the attention-related time ranges of the P90 and the N140 following tactile stimuli at the effector finger compared to a still non-effector finger of the other hand (Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer et al., 2006; Gherri & Forster, 2012a, 2012b). To dissociate the movement goal from the effector, Forster and Eimer (2007) let their participants execute pointing movements with one hand to the other and presented tactile stimuli to either one of the hands (i.e. moving effector-hand or stationary goal-hand) during the movement planning. Somatosensory ERPs around the P90 and the N140 were more negative following stimuli at the effector than at the goal-hand, and the authors concluded that tactile attention was shifted selectively to the effector, and not to the movement goal (Forster & Eimer, 2007). However, it is also possible that movement planning induces a shift of tactile attention both to the effector and to the movement goal with both locations being differently weighted. Consequently, tactile processing could be enhanced, though to a lesser degree than at the effector, at the movement goal, when compared to a task-irrelevant neutral location. This possibility was tested in Experiments 6.1–6.3.

Touch is remapped from an initial skin-based anatomical representation into an external spatial code that is derived from integrating skin

location with the current posture of the stimulated body part. Attentional effects on somatosensory ERPs are regularly attenuated when anatomical and external reference frames are placed in conflict, as by means of hand crossing (Eimer et al., 2003; Röder et al., 2008). In contrast, hand crossing did not significantly modulate effects on somatosensory ERPs related to planning a finger lift, possibly indicating that motor planning leads to an encoding of spatial reference frames in an external reference frame only (Gherri & Forster, 2012a). However, planning a non-goal-directed movement does not dissociate between effector and movement goal (Gherri & Forster, 2012a; van Ede et al., 2015). If movement planning of a body part shifted tactile attention to the movement goal, it is not clear whether this attention shift would be encoded relative to an anatomical or to an external reference frame. These reference frames are investigated in the following by placing them in conflict by means of hand crossing, that is, placing the anatomical left hand in the right external space and vice versa. This chapter presents an electrophysiological study and two behavioral experiments. These studies investigated how movement planning affected tactile processing at the movement goal (Experiments 6.1–6.3a) and at the movement effector (Experiment 6.3b) in comparison to movement-irrelevant locations. In addition, the studies investigated whether effects related to movement planning were encoded relative to an anatomical or an external reference frame.

6.1 Experiment 6.1: Somatosensory ERPs and oscillatory activity during movement planning

In this experiment, the EEG was recorded while participants planned and executed a pointing movement in the direction towards the index or little finger of either hand using the tip of their nose. During movement planning, a task-irrelevant tactile stimulus was pseudo-randomly presented either to one of the little or index fingers; this stimulus could occur at the movement's goal or at the non-goal hand. Critically, to probe the involvement of anatomical and external reference frames, hands were held either in an uncrossed or in a crossed posture. Somatosensory ERPs as well as oscillatory frequency bands related to movement planning and hand posture were analyzed. Preliminary ERP analysis of 12 subjects had indicated that somatosensory ERPs elicited by tactile stimuli at the goal-hand compared to at the non-goal hand were more positive in the range of

180 to 300 ms post-stimulus with uncrossed but not with crossed hands (Schubert, 2011), suggesting that movement-related ERPs were modulated by an external spatial reference frame. Yet, despite thorough artifact rejection of eye blinks on a single trial level, it appeared that ERP effects related to movement planning depended on horizontal eye drifts (Fig. 6.1C; Schubert, 2011). In the present analysis, this confound was removed, and ERP activity related to eye-movements was corrected using independent component analysis (Chaumon, Bishop, & Busch, 2015; Makeig, Debener, Onton, & Delorme, 2004). In addition, oscillatory EEG activity was analyzed to investigate which frequency bands may be involved in encoding possible attention shifts related to movement planning and to test how anatomical and external reference frames would be reflected in oscillatory activity. During the orientation of tactile attention (Chapter 3; Schubert et al., 2015), during attention-related tactile processing (Chapter 4) and during the planning of eye and hand movements to remembered tactile targets (Buchholz et al., 2011, 2013), external and anatomical reference frames have been associated with alpha- and beta-band activity, respectively. Thus, if indeed an attentional shift related to goal-directed movement planning was coded in anatomical and external spatial reference frames, then this attentional shift as well as a modulation of this effect by spatial reference frames should be reflected in corresponding modulations of oscillatory alpha- and beta-band activity.

6.1.1 Methods

Previously, methods and partial ERP results from this data set have been described in an unpublished master thesis (Schubert, 2011). The data set was acquired in a group of normally sighted participants (see below). Additionally, the data set contains data from eleven congenitally blind participants acquired in the context of the present thesis. Given that the spatial processing of touch critically depends on developmental vision (see Chapter 2 for an overview), hypothesized effects of movement planning and hand posture on tactile processing were expected to be modulated by the presence and absence of developmental vision. Yet, hypothesized effects in the sighted group were not observed, and hypotheses related to these effects in the blind group could not be investigated. The data of the blind group are therefore not reported here.

6.1.1.1 Participants

Data of twelve sighted participants (5 female, mean age = 28.4, range between 21 and 49 years) was used for data analysis. Data of four additional participants was excluded due to a large number of EEG artifacts and premature responses in more than one third of the trials (3 participants) and due to technical problems (1 participant). All participants were neurologically healthy by self-report and had normal or corrected-to-normal vision. Participants gave written informed consent before data collection and received either course credit or 8 Euro per hour for participation. The study was approved by the German Psychological Society (TB 122010) and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2013).

6.1.1.2 Apparatus

Participants sat in a sound and electrically shielded chamber with their hands resting on a table in front of them. Hands were placed either in an uncrossed or crossed posture, varied in a blockwise fashion. Custom-built tactile stimulators were attached to the little and index fingers of both hands.

The distance between stimulators at the index (little) fingers was kept at approximately 10 cm with uncrossed (crossed) hands. To elicit a tactile stimulation, a small metal rod (diameter 1.5 mm) was lifted for 50 ms by 0.5 mm from its resting position (for a detailed description see Schicke & Röder, 2006). To mask sounds emitted by the stimulators, participants wore earplugs, and white noise was played via loudspeakers. All participants wore a blindfold and headphones, which were used to present auditory stimuli. Stimuli were controlled with Presentation 14.2 (Neurobehavioral Systems, Albany, CA). Head movements were measured with a camera-based movement tracking system (Optotrak Certus, Northern Digital Inc., Ontario, Canada) at a rate of 100 Hz controlled via Matlab. To this end, an LED marker was attached either on the chin or on the nose, depending on which position could be monitored best in each participant. The LED marker was placed on top of a small piece of aluminum attached to the skin with tape. Bending the aluminum piece allowed angling the marker towards the cameras of the motion tracker.

6.1.1.3 Procedure

Figure 6.1A illustrates the schematic structure of a trial. Participants were asked to point with their tip of the nose towards one of their little or index fingers and to ignore any tactile stimuli. Using little and index fingers as movement goals in different trials allowed assessing whether participants executed goal-directed movements to one of their fingers rather than non-goal-directed left-right movements. At the beginning of each trial, the German words “links” (left) or “rechts” (right) were presented via headphones to indicate whether the movement goal was at the left or the right hand, irrespective of its location in space. Volume and duration (300 ms) were adjusted to be equal for all auditory stimuli. The words were spoken by a female and by a male speaker. The sex of the speaker indicated to the participants whether the movement goal was the little or the index finger. The speaker-finger mapping was counterbalanced across participants. In 90 % of the trials, a tactile stimulus was randomly presented 600 to 900 ms after the verbal cue onset to one of the four possible movement targets.

The remaining 10% of trials served as “filler trials” and did not contain any tactile stimulation. An auditory go-cue (100 ms, 900 Hz sine wave) was presented 300-400 ms after tactile stimulus onset and instructed the participant to move as fast as possible to the cued location. Participants were asked to execute fast rotating head movements and to rotate the head back to the center after pointing to the movement goal with their nose. The time between go-cue and beginning of the next trial was randomized between 1300 and 1700 ms. Participants completed sixteen blocks of 71 trials with a total of 1136 trials (32 trials per condition, 112 filler trials). Hand posture was changed after every other block. Half of the participants started with uncrossed hands, the other half with crossed hands. At the beginning of the experiment, participants completed one practice block in each hand posture.

6.1.1.4 EEG recording

EEG was recorded from 74 passive AG/AgCl electrodes (Fig 6.1B) with BrainVision Recorder (Brain Products GmbH, Gilching, Germany) at 500 Hz with an analog band-pass filter between 0.1 Hz and 250 Hz. Electrodes were placed according to the 10-10system (Oostenveld & Praamstra, 2001): FPz, FP1/2, AFz, AF3/4, AF7/8, Fz, F1/2, F3/4, F5/6, F7/8, F9/10, FCz, FC1/2, FC3/4, FC5/6, FT7/8, FT9/10, Cz, C1/2, C3/4, C5/6, T7/8, CPz, CP1/2, CP3/4, CP5/6, TP7/8, TP9/10, Pz, P1/2, P3/4,

P5/6, P7/8, P9/10, POz, PO3/4, PO7/8, PO9/10, Oz, O1/2, O9/10 and Iz. The common reference was provided by a right earlobe recording. Vertical eye movements were recorded with an electrode underneath the right eye. Horizontal eye movements were calculated offline by the difference between F9 and F10 electrodes (HEOG). Electrode impedances were kept below 5 k Ω .

6.1.1.5 Design

The experimental design comprised the within-subject factors Posture (uncrossed vs. crossed), Stimulated Hand (left vs. right), Stimulated Finger (little vs. index), Cued Hand (left vs. right), and Cued Finger (little vs. index). In order to increase signal-to-noise ratio and to ease interpretability of the analysis, data were collapsed across fingers and across hands by averaging activity elicited by tactile stimuli presented to fingers of one hand and by recoding electrode positions into electrode positions ipsi- and contralateral relative to stimulated hand, irrespective of the hand position. Thus, the design of the actual analysis contained only the within-factors Posture (uncrossed vs. crossed) and Movement Goal (goal hand vs. non-goal hand).

6.1.1.6 Data analysis

Movement data was analyzed using Matlab (MathWorks Inc., Natick, MA, USA). Each trial was visually inspected and rejected if movements along the x-axis, defined as the horizontal left-right dimension relative to the participant (see Fig. 6.6A for the definition of spatial axes), indicated a premature head movement onset before presentation of the auditory go-cue (for a detailed description see Schubert, 2011). EEG data was processed using EEGLAB (Delorme & Makeig, 2004) and FieldTrip toolboxes (Oostenveld et al., 2011) within the Matlab environment. Data were band-pass filtered offline between 0.3 and 110 Hz. Next, data were down-sampled to a sampling rate of 250 Hz to shorten data processing to a reasonable time for a subsequent independent component analysis. Epochs with extensive movement and muscle artifacts were deleted after visual inspection. Because HEOG activity indicated that horizontal eye drifts differed significantly between experimental conditions (Fig. 6.1C), an independent component analysis (ICA) was conducted to remove EEG components related to eye movements (Chaumon et al., 2015; Makeig et al., 2004). Finally, data were segmented into epochs lasting from 300 ms pre-

stimulus until 300 ms post-stimulus relative to tactile stimulus onset. Selecting this time window avoided any overlap with auditory movement-goal and go-cues (Fig. 6.1A).

6.1.1.7 Analysis of somatosensory ERPs

Data were re-referenced offline to a linked earlobe reference to allow direct comparison to previous research (e.g. Gherrri & Forster, 2012a). ERP activity was corrected relative to a 100 ms baseline preceding tactile stimulus onset. Data measured at single electrodes were aggregated into electrode clusters, each comprising three electrodes (Fig. 6.1B). For each participant and condition, mean amplitude values were computed at each cluster for three post-stimulus time windows 76-110 ms, 116-140 ms, and 180-300 ms (see Fig. 6.1C,D for a visualization of these time windows). Time windows were selected after visual inspection to capture the peaks of ERP amplitudes. These averages were entered in an ANOVA for repeated measures with within-subject factors Hemisphere (ipsi- vs. contralateral), Cluster (7 clusters; Fig. 6.1B), Posture (uncrossed vs. crossed), and Movement Goal (goal hand vs. non-goal hand) for each time window. Degrees of freedom and p-values were Greenhouse-Geisser corrected when appropriate, but original degrees of freedom are reported with corrected p-values. When interactions between the relevant factors and clusters were found, additional analyses were conducted for single clusters.

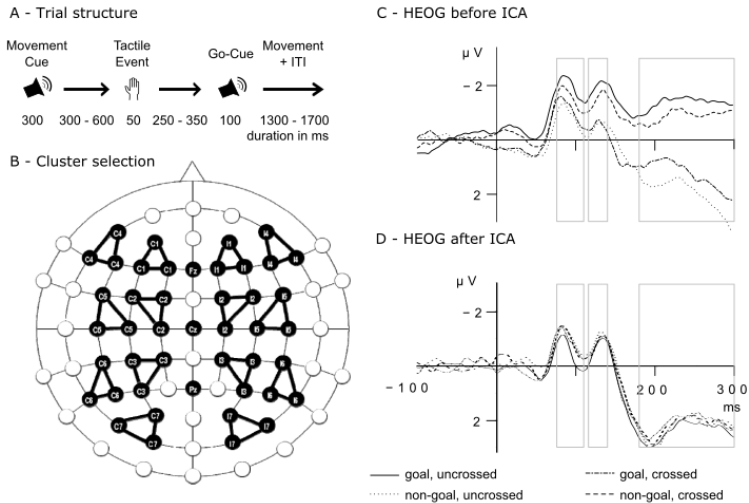


Figure 6.1. Experiment 6.1.

A. Schematic trial structure of a trial containing a tactile event. Participants held their hands either in an uncrossed or crossed posture (blockwise manipulation). At the beginning of each trial an auditory cue indicated the movement goal (left/right index/little finger). After 300 to 600 ms following the movement cue a tactile stimulus was presented to one of the possible movement goals. Following the tactile stimulus an auditory Go-cue signaled to the participants to execute the cued movement. See section 6.1.1.3 for details. **B.** Electrode positions and cluster selection for ERP analysis. Each cluster consisted of 3 electrodes, as marked here with black triangles. Contralateral clusters are named C1-7, ipsilateral clusters I1-7. For orientation, midline electrodes Fz, Cz, and Pz are indicated, but were not used in the analysis. **C, D.** Horizontal electro-oculogram (HEOG) with uncrossed (black) and crossed hands (red) time-locked to stimuli at the goal hand (solid lines) and at the non-goal hand (dotted lines) relative to the cued nose movement. The HEOG was derived by subtracting EEG activity at electrode F9 from activity at electrode F10. The figures show the HEOG before (**C**) and after (**D**) correction of EEG activity by means of an independent component analysis (ICA), which removed activity related to eye movements. Gray rectangles mark the time periods that were used for statistical analysis. Panel **C** is adapted from Schubert (2011).

6.1.1.8 Frequency analysis

For frequency analysis, data were re-referenced to an average reference, and line noise was removed by a notch filter centered at 50 Hz. Data were then transformed into the spectral domain using Morlet wavelets (M. X. Cohen, 2014) with sliding windows of 20 ms step size. The width of the wavelets was linearly increased from 4 cycles at 2 Hz up to 13 cycles at 100 Hz. Oscillatory activity in the time window centered around 160 ms pre-stimulus served as a baseline. Oscillatory activity was normalized by the baseline activity, resulting in percent signal change from baseline:

$$\text{activity} = 100 \frac{\text{power} - \text{baseline}}{\text{baseline}}.$$

6.1.1.9 Non-parametric cluster-based permutation statistics

Oscillatory activity was compared between conditions using non-parametric cluster-based permutation tests (CBPT) to control for multiple comparisons (Maris & Oostenveld, 2007). This procedure included paired t-tests at each data sample (i.e. at each electrode, each time point, and each frequency bin). Next, cluster candidates were obtained by thresholding samples depending on the p-value ($p < 0.05$) as derived with the t-tests. Only samples with p-values below threshold and at least two samples with p-values below threshold neighboring in time, frequency, and space (i.e. electrode position) were included into clusters. Cluster descriptives (i.e. t-values) were summed and used as a single cluster statistic. This observed cluster statistic was compared with a permutation distribution, which was derived by shuffling conditions 1000 times and by calculating cluster statistics for each permutation. Thus, the CPBT tests the null-hypothesis of exchangeability between conditions (Maris & Oostenveld, 2007). Reported p-values refer to the percentile of the observed cluster statistics in comparison to the permutation distribution. The CBPT does not trivially transfer to testing interactions between experimental factors. To test the interaction between the factors Posture and Movement Goal the difference between activity with uncrossed and activity with crossed hands was calculated separately for each Movement Goal condition. Subsequently, these differences were tested with a CBPT.

6.1.2 Results

Grand averages of somatosensory ERPs for the main effects of Movement Goal and Posture are shown in Fig. 6.2 and 6.3, respectively.

6.1.2.1 Event-related potentials: 76-110 ms

The ANOVA with factors Hemisphere, Cluster, Posture, and Movement Goal revealed a significant main effect for Cluster ($F(6, 6) = 7.18, p = 0.001$), a two-way interaction between Hemisphere and Cluster ($F(6, 66) = 4.83, p = 0.010$), a trend for an interaction between Cluster and Movement Goal ($F(6, 66) = 2.55, p = 0.082$). Following up on the trend for an interaction between Cluster and Movement Goal, post-hoc comparisons revealed that ERPs were significantly more positive following tactile stimuli presented at the goal hand than at the non-goal hand at clusters C1/I1 ($F(1, 11) = 8.91, p = 0.012$) and C2/I2 ($F(1, 11) = 5.52, p = 0.039$). Note that for these post-hoc tests data were collapsed across ipsi- and contralateral clusters; when testing these clusters separately at ipsi- and contralateral sites, an effect of Movement Goal was only present at ipsilateral clusters I1 and I2. Yet, the relation to laterality must be interpreted with caution, because a higher order interaction between Hemisphere, Cluster, and Movement Goal was not significant ($F < 1$), precluding further comparison across conditions. Moreover, a trend for an interaction between Hemisphere and Posture was observed ($F(1, 11) = 3.22, p = 0.100$; note that the p-value was rounded and $p < 0.1$). Following up on this trend yielded a trend for a more positive ERP with uncrossed than crossed hands in the ipsilateral ($F(1, 11) = 3.31, p = 0.096$), but not in the contralateral hemisphere ($F < 1$).

In sum, somatosensory ERPs showed a trend to be modulated by hand posture and movement planning in the time window between 76 and 110 ms. ERPs elicited by tactile stimuli at the goal-hand compared to at the non-goal hand were marginally more positive at frontal and central electrode clusters (marked with gray rectangles in Fig. 6.2). Hand posture marginally influenced somatosensory ERPs in that time window in the ipsilateral hemisphere with more positive ERPs with uncrossed than crossed hands.

6.1.2.2 Event-related potentials: 116-140 ms

In the time window between 116 and 140 ms, the ANOVA with factors Hemisphere, Cluster, Posture, and Movement Goal revealed a

significant main effect for Hemisphere ($F(1, 11) = 6.11, p = 0.031$) and for Cluster ($F(6, 66) = 4.48, p = 0.006$). No significant interactions with Posture and Movement Goal were observed (all $p \geq 0.209$). A trend for a main effect of Movement Goal was observed with more positive ERPs following tactile stimuli at the goal than non-goal hand ($F(1, 11) = 3.98, p = 0.071$).

6.1.2.3 Event-related potentials: 180-300 ms

The ANOVA with factors Hemisphere, Cluster, Posture, and Movement Goal revealed main effects for Hemisphere ($F(1,11) = 10.23, p = 0.008$) and for Cluster ($F(6, 66) = 8.22, p = 0.002$), an interaction between Cluster and Movement Goal ($F(6, 66) = 8.24, p = 0.001$), an interaction between Cluster and Posture ($F(6, 66) = 4.44, p = 0.019$), and an interaction between Hemisphere and Cluster ($F(6, 66) = 9.28, p < 0.001$). To resolve these multiple interactions, post-hoc comparisons compared Movement Goal effects for each of the ipsi- and contralateral clusters. These tests revealed that ERPs were significantly more positive for tactile stimuli when presented at the goal hand than at the non-goal hand at contralateral clusters C1 ($F(1, 11) = 12.91, p = 0.004$) and C2 ($F(1, 11) = 5.63, p = 0.037$) and at ipsilateral clusters I1 ($F(1, 11) = 11.27, p = 0.006$), I2 ($F(1, 11) = 6.03, p = 0.032$), and I4 ($F(1, 11) = 11.49, p = 0.006$). A trend in the same direction was observed at cluster I5 ($F(1, 11) = 4.65, p = 0.054$). Moreover, post-hoc comparisons testing the origin of the interaction between Cluster and Posture revealed that somatosensory ERPs were marginally more positive with uncrossed than with crossed hands at clusters C2/I2 ($F(1, 11) = 4.81, p = 0.051$) and C3/I3 ($F(1, 11) = 4.08, p = 0.069$), but not at other clusters ($p > 0.1$). The analysis did not reveal significant interactions between Posture and Movement Goal or between these two factors and Hemisphere or Cluster (all $p \geq 0.114$). In sum, somatosensory ERPs elicited by tactile stimuli at the goal hand compared to at the non-goal hand were more positive at frontal and central electrode clusters in the time window between 180 and 300 ms. Moreover, ERPs were marginally more positive with uncrossed than with crossed hands at central and parietal clusters in this time window.

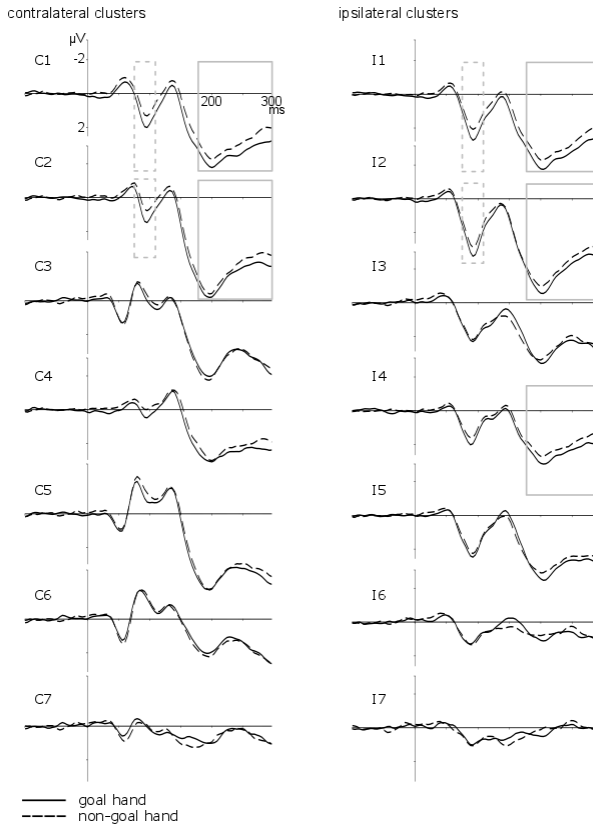


Figure 6.2. Experiment 6.1. Grand average somatosensory ERPs elicited by tactile stimuli presented at the goal-hand (solid lines) and at the non-goal hand (dashed lines) at electrode clusters contralateral (left column) and ipsilateral (right column) relative to the tactile stimulus (for cluster locations see Fig. 6.1B). Activity was averaged across posture conditions. Gray rectangles mark clusters and time windows, during which movement planning modulated EEG activity ($p < 0.05$, solid gray; $p < 0.1$, dashed gray; see 6.1.2 for details).

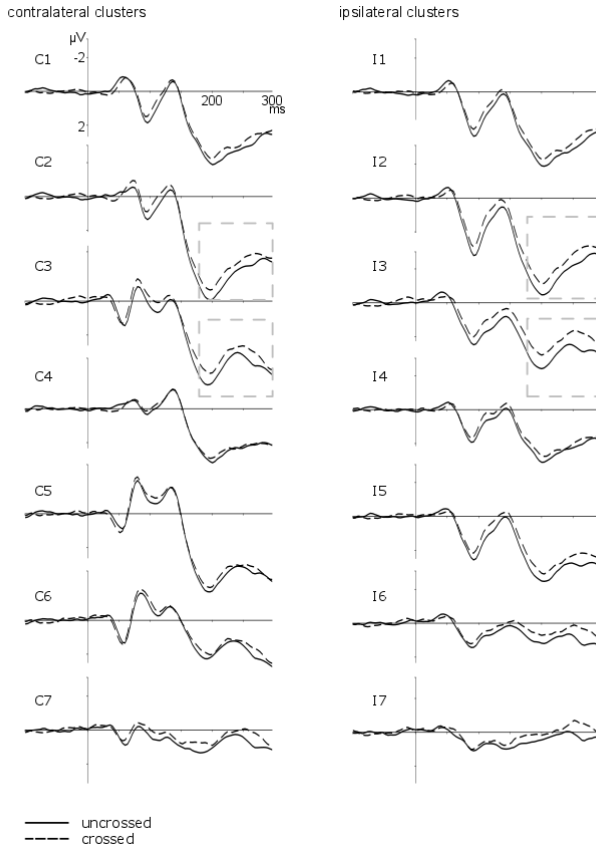


Figure 6.3. Experiment 6.1. Grand averaged somatosensory ERPs elicited by tactile stimuli with uncrossed (solid lines) and crossed hands (dashed lines) for clusters anatomically (that is, irrespective of hand posture) contralateral (left) and ipsilateral (right) relative to the tactile stimulus (for cluster locations see Fig. 6.1B). Activity was averaged across movement conditions. Gray rectangles mark clusters and time windows, during which hand posture marginally modulated EEG activity ($p < 0.1$; see 6.1.2 for details).

6.1.2.4 Oscillatory activity

Tactile stimuli suppressed oscillatory activity relative to baseline between 10 and 35 Hz, that is, in the range of the alpha-and beta-bands (Fig. 6.4C, F; cluster-based permutation test: $p = 0.004$). This effect was evident over a large portion of the scalp at numerous electrodes (marked with plus signs in Fig. 6.4F). Suppression was at its maximum at approximately 20 Hz after 250 ms.

Oscillatory activity induced by tactile stimuli at the goal-hand compared to tactile stimuli at the non-goal hand did not differ significantly (CBPT: $p = 0.205$). Similarly, hand posture had no significant effect on oscillatory activity (CBPT: $p = 0.201$). Moreover, no significant interactions between Posture and Movement Goal were observed (CBPT: $p = 0.396$). Fig. 6.4 shows oscillatory activity elicited by tactile stimulation for all experimental conditions.

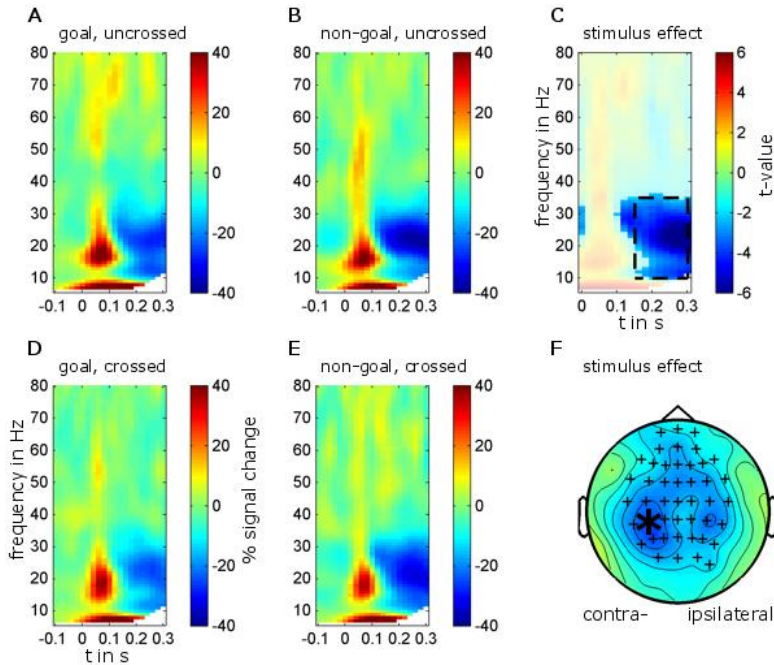


Figure 6.4. Experiment 6.1. Oscillatory activity elicited by tactile stimulation at the contralateral electrode CP3/4 (marked with an asterisk in F). **A, B, D, E.** Activity is shown following tactile stimuli at the goal hand (**A, D**) and at the non-goal hand (**B, E**) with uncrossed (**A, B**) and crossed hands (**D, E**). Data at long latencies for low frequencies is unavailable as a consequence of larger analysis windows for low frequencies. **C.** Oscillatory activity was collapsed across conditions and compared with baseline activity (cluster-based permutation test: $p = 0.004$). Significant clusters are nontransparent. **F.** Topography of 10-35 Hz activity between 150 and 300 ms post-stimulus (marked with a black rectangle in C); colors are scaled as in C. The left side is contralateral to tactile stimulation. Plus signs and asterisk mark electrodes at which oscillatory activity was significantly suppressed compared to baseline.

6.1.3 Discussion Experiment 6.1: EEG study

The present study investigated whether processing of task-irrelevant tactile stimuli is enhanced when the stimulated region is the goal location of a nose-pointing movement. In addition, the study investigated whether such planning-related effects operated in an anatomical or in an external spatial reference frame. Somatosensory ERPs elicited by tactile stimuli at the goal hand were significantly more positive than ERPs elicited by tactile stimuli at the non-goal hand, evident at frontal and central electrode clusters in the time range between 180 and 300 ms. Hand posture did not significantly modulate this effect related to movement planning. Hand posture only marginally influenced somatosensory ERPs, independent of movement planning. Oscillatory EEG activity was suppressed following tactile stimulation in the alpha- and beta-band range over a large part of the scalp. Yet, oscillatory activity was not significantly modulated by movement planning or hand posture.

Modulation of somatosensory ERPs by movement planning and hand posture

The observed movement planning effect on somatosensory ERPs beyond 180 ms, with more positive ERPs at the goal than at the non-goal hand, is not easily interpreted in the context of previous findings on covert tactile attention. Previous studies reported attention-related ERP effects in the opposite direction in this time period, with more negative ERPs following attended than unattended tactile stimuli (e.g. Eimer & Forster, 2003; Gherri & Forster, 2012a; Röder et al., 2008). In addition, studies investigating effects of saccadic or finger lift movement planning on somatosensory ERPs have not reported any significant effects for this time window (Eimer et al., 2005; Gherri & Eimer, 2008; Gherri & Forster, 2012a, 2012b). Only when visually assessing the study by Eimer and colleagues (2005), ERP traces between 200 and 300 ms appear to be deflected in the same direction as in the present study, although no statistical tests for this time period were reported. The difference in this late ERP time window between paradigms investigating covert tactile attention versus paradigms investigating movement planning might either reflect differences in the task-relevance of the tactile stimuli which arise at later processing stages (Gherri & Forster, 2012a), or a difference in how attention is deployed between paradigms. It has been argued that the similarity between enhancements of somatosensory

ERPs at earlier time ranges (i.e. P100, N140) by both covert tactile attention (Eimer & Forster, 2003; Michie et al., 1987) and motor planning of a finger lift support the premotor theory of attention (Eimer et al., 2005). Yet, in the present study only a trend for an enhancement of somatosensory ERPs in the time range of the P100 was observed. One could speculate that the marginal significance is due to a lack of power, given the relatively low number of participants (N=12), and that significance may have been obtained with a larger sample. If one follows this reasoning, then the trend for significance could be tentatively interpreted as reflecting a shift of tactile attention towards the movement goal and, thus, would then support of the premotor theory of attention as well. The effect of goal-directed movement planning on tactile processing at the movement goal compared to the effector may, however, be smaller (Forster & Eimer, 2007). Alternatively, the present findings could be interpreted as evidence against the premotor theory of attention's proposal that a shared neural mechanism guides movement planning and attentional deployment (Rizzolatti et al., 1987, 1994). If these neural mechanisms were indeed identical, then one would expect that ERP effects related to covert attention shifts, as reported in previous studies, and the present effects related to goal-directed movement-planning should be comparable. In the present study, this was only true for the time window of the P100 (76 – 110 ms), during which at least a trend was observed in the expected direction. Thus, the present findings could be rather compatible with the idea that attention and movement planning are mediated by anatomically distinct, but presumably closely linked mechanisms, than with the claim that one and the same neural mechanism guides attention and movement planning.

Indeed, in the visual modality two distinct mechanisms have been proposed to govern the directing of attention in the context of covert spatial orienting and movement preparation, based on the additive amplitude modulation of visual ERPs between 170 and 220 ms poststimulus (N1) by covert spatial attention and manual movement planning (Ley & Röder, 2014). The existence of separate systems is further suggested by the notion that covert tactile attention and attentional shifts related to movement planning appear to be related to anatomical and external spatial reference frames via different mechanisms: For covert tactile attention, hand crossing has been reported to attenuate attention effects on somatosensory ERPs (Eardley

& van Velzen, 2011; Eimer et al., 2003; Gherri & Forster, 2012a; Heed & Röder, 2010; Röder et al., 2008), presumably indicating a conflict between anatomical and external spatial coordinates. In contrast, somatosensory ERPs do not appear to be modulated by hand crossing during movement planning either in preparation of a saccade or a finger lift (Gherri & Forster, 2012a, 2012b). In addition, planning a saccade decreases reaction times to tactile stimuli at the hand that coincides with the saccade goal in external space, but not the other hand (Rorden et al., 2002). Critically, this effect did not significantly differ between uncrossed and crossed hands (Rorden et al., 2002), suggesting that attentional shifts related to movement planning may preferably operate in an external spatial reference frame. Similarly, effects related to movement planning in the present study were not modulated by hand posture. However, because movement cues and the coding of the effects during the analysis were defined relative to anatomical space, the present finding may indicate that that anatomical information was weighted more strongly than external information. This contrasts previous studies, in which movement cues referred to external space, and which reported effects that were determined by the external location of the stimulus (Gherri & Forster, 2012a, 2012b; Rorden et al., 2002). This contrast between studies may, thus, be related to the differences in spatial cueing. Nevertheless, the absence of hand posture effects in the present and in previous studies suggests that, although the underlying brain mechanisms of spatial attention and movement planning may be linked to some extent, they appear to be linked in a different fashion to anatomical and external reference frames.

Tactile stimulation suppressed alpha- and beta-band activity

Consistent with previous findings (Bauer et al., 2006; Crone et al., 1998; Nikouline et al., 2000; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997) tactile stimuli in the present study suppressed oscillatory activity in the alpha- and beta-band range widespread over bilateral electrodes with the largest suppression at central contralateral electrodes. This effect has been suggested to originate primarily in sensorimotor areas (Crone et al., 1998), the ipsilateral somatosensory cortex, as well as bilateral parietal and occipital areas (Bauer et al., 2006). However, in the present study the experimental manipulations of hand posture and location of the movement goal relative to tactile stimulation did not significantly modulate oscillatory activity. There are several possibilities that may

account for this observation. First, the study design was optimized to capture effects on somatosensory ERPs, resulting in short time intervals available for frequency analysis (300 ms rather than usually 1000 ms or more). Whereas a short analysis window is unproblematic for higher frequency bands, it most probably distorts the estimation of low frequency bands, as only a low number of cycles can be fitted. For example, despite having an artifact free time window of only 300 ms, we used a time window of 500 ms (approximately 5 cycles) to achieve reliable power estimation in the range of the alpha-band. Thus, the power estimation for low frequencies may have been contaminated with prestimulus activity. Moreover, largest effects of tactile attention on occipital alpha- and beta-band activity have been reported to peak around 400 ms after stimulus onset (Bauer et al., 2006), a time point beyond the 300ms time window available in the present design. Second, in contrast to paradigms that investigated covert tactile attention (e.g. Bauer et al., 2006) tactile stimuli were not task-relevant in the present study. It is thus possible that task-relevance may emphasize modulations of oscillatory activity by tactile attention. However, it is also possible that the link between movement planning and shifts of tactile spatial attention to the movement goal is rather weak and that effects of movement planning on tactile processing are observed rather at the effector than at the movement goal (cf. Forster & Eimer, 2007). In sum, the findings of the present EEG study suggest that movement planning and shifts of spatial attention are at least partially linked, as evident in the modulations of the somatosensory ERPs. Yet, posture and movement planning did not significantly modulate oscillatory activity. Possible reasons for these negative findings may be that tactile stimuli were task-irrelevant in the present experimental design or that the link between movement planning with the nose and shifts of tactile spatial attention is rather weak.

6.2 Experiment 6.2: tactile discrimination during movement planning at the movement goal

One drawback of the EEG design used in Experiment 6.1 is that EEG modulations elicited by task-irrelevant tactile probes were studied, which does not allow obtaining a behavioral measure. Therefore, we designed an additional behavioral experiment. This experiment closely matched the experimental conditions of the EEG study, but rendered behavioral measures to assess effects of posture and motor planning. As

in the EEG study, participants planned and executed pointing movements with their nose to their index and little fingers of both hands. Shortly before the movement, a tactile target stimulus was presented at one of these fingers. In contrast to the EEG study, this target stimulus was task-relevant and a discrimination judgement about the tactile stimulus had to be given at the end of the head movement.

We hypothesized that the planning of a head pointing movement enhances tactile discrimination performance at the goal hand compared to the non-goal hand. Such an effect would indicate that head movement planning leads to a shift of tactile spatial attention to the movement goal similar to planning a saccade (Juravle & Deubel, 2009; Rorden et al., 2002). Moreover, whether such a shift of tactile spatial attention operates in an anatomical or in an external spatial reference frame was tested by crossing the hands. If both anatomical and external integration is integrated for tactile attention shifts related to movement planning, then effects of movement planning should be reduced by hand crossing as anatomical and external information are in conflict.

6.2.1 Methods

6.2.1.1 Participants

From a total of 31 tested participants, data of seventeen participants (9 female, all right-handed, mean age: 25.7 years; age range from 19 to 39 years) were included in the analyses. Data of fourteen participants were discarded due to the following reasons: five participants misunderstood response instructions (i.e. they gave a large number of premature responses, were confused about the response coding in the course of the experiment, or ignored parts of the instruction), two participants decided to abort the experiment, two participants were excluded due to technical reasons, and five participants responded at chance level. All participants were neurologically healthy by self-report and had normal or corrected-to-normal vision. All participants provided informed written consent and received course credit or monetary reimbursement for participation (7 Euro/h). The study was approved by the German Psychological Society (TB 122010) and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2013).

6.2.1.2 Apparatus and stimuli

The apparatus was identical to Experiment 6.1. For tactile target stimuli, stimulator pins were lifted either two or three times (50 ms each), presented with a stimulus onset asynchrony of 100 ms. Whether stimulator pins were lifted two or three times was randomly determined in each trial.

6.2.1.3 Procedure

As in Experiment 6.1, participants were asked to point with their nose in the direction towards one of their index or little fingers. Using little and index fingers as movement goals in different trials allowed differentiating goal-directed movements and non-goal-directed left-right movements. Instructions for movements and directional auditory cues were the same as in Experiment 6.1.

Following the directional auditory cue, a tactile target stimulus was randomly presented to one of the four locations after 600 to 900 ms. Then, 300 – 400 ms following the tactile stimulus onset, an auditory go-cue (100 ms, sine wave, 900 Hz) indicated to initiate the pointing movement. After movement completion, participants had to report whether they had perceived two or three touches by lifting either the toes or the heel off a response pedal under the left (right) foot (counterbalanced across participants). The response mapping was counterbalanced across participants. The next trial started 300 to 600 ms after a foot response was recorded. In case no head movement was detected (i.e. a deviation from the starting position of more than 2 cm), the trial was repeated at a random time point within the remaining experimental block. Participants completed 512 trials divided into eight blocks of 64 trials. Hand posture was changed after every other block. Starting posture was counterbalanced across participants.

6.2.1.4 Practice

Before the beginning of the experiment participants practiced the head movement without any tactile stimulation until they were able to reliably initiate the movement within 700 ms after go-cue onset. Afterwards, they practiced the task itself with head movements towards the cued location and responses to perceived tactile stimulation. Participants completed at least one practice block (i.e. 64 trials).

6.2.1.5 Design

The experiment contained five factors: Posture (uncrossed vs crossed), Cued Hand (left vs. right), Cued Finger (little vs. index finger), Stimulated Hand (left vs. right), and Stimulated Finger (little vs. index finger). For statistical analysis, the stimulus locations were re-defined relative to the movement goal by the factors Hand (goal vs. non-goal hand) and Finger (goal vs. non-goal finger), resulting in a 2 x 2 x 2 design, that is, Posture x Hand x Finger.

6.2.1.6 Data analysis

Movement data was analyzed along the left-right dimension, labeled x-axis, relative to the participant's body (for definition of spatial axes see Fig. 6.6A). For each condition, the mean and the standard deviation of the most eccentric movement points along the x-axis over time were calculated across trials. Movement traces along the x-axis of each trial were visually compared to the corresponding mean and rejected if the most eccentric point of the trial exceeded the mean of the current condition by two standard deviations, and if movements along the x-axis over time indicated that the movement was initially executed into the wrong direction (6.5% of all trials).

Accuracy was analyzed in R (version 3.2.2; R Core Team, 2015) using the R packages lme4 (v1.1-9; Bates et al., 2014), afex (v0.14.2; Singmann et al., 2015), lsmeans (v2.20-2; Lenth & Hervé, 2015), dplyr (v0.4.3; Wickham & Francois, 2015), and visualized with ggplot2 (v1.0.1; Wickham, 2009). Trials were excluded if reaction times were shorter than 150 ms, if participants failed to respond, or if participants simultaneously lifted both the heel and the toes from the foot pedal (5.1 % of all trials). Only accuracy rates, but not reaction times, were analyzed, because participants were asked to execute the pointing movement and to give an unspeeded response after movement completion.

6.2.1.7 Generalized mixed model analysis

For categorical data, it has been suggested that using an ANOVA is inappropriate, because this approach contains several serious problems: for instance, the variances in two binomially distributed conditions will in general not be homogeneous—contrary to the assumption of an ANOVA (Jaeger, 2008). Thus, a generalized linear mixed model (GLMM) with a binomial link function was used to analyze accuracy data to

overcome shortcomings of the ANOVA approach (Bolker et al., 2009). Participants' data were entered as random effects. The fitted and reliably converging model comprised random intercepts and slopes for each main effect and for all two-way interactions. Some of the correlations for the participant random effects were quite high (± 0.7), potentially indicating an overparametrization of the model (Bates, Kliegl, Vasishth, & Baayen, 2015).

Consequently, the estimation of correlations between random effects was suppressed in the final model (Singmann, submitted). Significance of fixed effects was assessed by means of comparing the model with the maximal fixed effects structure and a reduced model without the fixed effect of interest using likelihood ratio tests (Pinheiro & Bates, 2000). This analysis was performed with the *afex* package, employing type III sums of squares and sum-to-zero contrasts (Singmann et al., 2015). Fixed effects were considered to be significant for $p < 0.05$. Post-hoc comparisons of significant interactions were conducted using approximate z-tests on the estimated least square means (Lenth & Hervé, 2015). Holm adjustments were used to correct for multiple comparisons (Holm, 1979). The GLMM was fitted with the fixed within-subject factors Posture (uncrossed vs. crossed), Hand (goal vs. non-goal hand), and Finger (goal vs. non-goal finger).

6.2.2 Experiment 6.2: Results

Model estimates of the GLMM are depicted in Fig. 6.5. A result overview of the GLMM is shown in Table 6.1. There was a significant main effect for Posture ($\chi^2(1) = 7.43$, $p = 0.006$) with more accurate responses with uncrossed than with crossed hands and a trend for an interaction between Posture and Hand ($\chi^2(1) = 3.29$, $p = 0.070$). Post-hoc comparisons following up on this trend revealed that participants responded marginally more accurate to tactile targets presented to the goal hand than to the non-goal hand with uncrossed hands ($z = 2.23$, $p = 0.052$; Holm corrected), but not with crossed hands ($z = -0.33$, $p = 0.737$). No significant effects of Finger or interactions with Finger were revealed by the GLMM (Table 6.1).

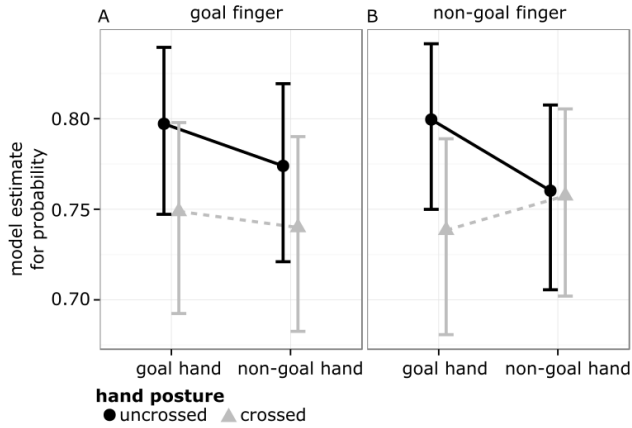


Figure 6.5. Experiment 6.2. Model estimates derived from the generalized linear mixed model (GLMM). **A, B.** Estimated probability to correctly discriminate tactile stimuli presented to the goal (left in each panel) and to the non-goal hand (right in each panel) with uncrossed (black circles) and crossed hands (gray triangles) are shown for stimuli presented to the same/analogous (**A**) or to the non-goal finger (**B**) relative to the goal finger of the movement. Whiskers represent 95 % confidence intervals and are asymmetric because the GLMM used a logit link function; accordingly, values appear compressed for high and low probability values when back-transformed into the original probability scale.

Table 6.1. Experiment 6.2. Results of the GLMM for accuracy. Coefficients are logits. Bold font indicates $p < 0.05$.

Predictor	Estimate	χ^2	df	p
(intercept)	1.181	-	-	-
Posture	-0.103	7.43	1	0.006
Hand	-0.039	1.58	1	0.209
Finger	-0.003	0.01	1	0.914
Posture X Hand	0.053	3.29	1	0.070
Posture X Finger	0.013	0.21	1	0.645
Hand X Finger	0.007	0.07	1	0.795
Posture X Hand X Finger	0.030	1.22	1	0.269

6.2.3 Experiment 6.2: Discussion

The experiment was designed to assess whether movement planning enhances tactile perception at the movement goal and in which spatial reference frames such an enhancement might operate. Participants discriminated tactile target stimuli presented at one of their little or index fingers during the planning of a pointing movement with the nose towards one of the little or index fingers. To investigate the involved spatial reference frames of movement-related attentional shifts, hands were placed either in an uncrossed or a crossed posture. Participants responded significantly more accurately with uncrossed than with crossed hands. Planning a pointing movement with the nose towards a finger of one hand marginally enhanced the accuracy of tactile discrimination at the goal-hand compared to the non-goal hand. This trend for an effect was only observed with uncrossed, but not with crossed hands.

It was hypothesized that head movement planning enhances tactile discrimination performance at the goal hand compared to the non-goal hand. Such an observation would have corroborated previous reports on saccades: planning a saccade to one of the hands shortens reaction times both for tactile localization (Rorden et al., 2002) and for the detection of an intensity change of a vibrotactile stimulus at the goal-hand compared to the other hand (Juravle & Deubel, 2009). However, in the present experiment movement planning influenced tactile discrimination performance with uncrossed hands only marginally, providing little evidence in support of our hypothesis. Additionally, interpretation of results is made more difficult by the rather high drop-out rate of participants, indicating that the task may have been quite demanding. Based on the current findings it is, thus, unclear whether tactile perception is enhanced at the goal location of a goal-directed movement with an effector other than the eyes.

It is noteworthy that the marginal effect of hand crossing on planning-related effects in the present study is in contrast to a study by Rorden and colleagues (2002): Planning a saccade to one of the hands similarly fastened localization responses to tactile stimuli at the goal-hand compared to the non-goal hand with uncrossed and crossed hands.

It was suggested that this finding indicates that saccade planning enhanced tactile processing at the external spatial location of the hands independent of hand posture (Rorden et al., 2002). At least three differences between these studies may account for the observed trend

of an effect of hand crossing in the present study. First, non-informative vision of the hands emphasizes the weighting of external spatial information (Newport et al., 2002). Vision was not available in the present head pointing task. Second, although head and eye-movements may similarly enhance tactile processing at the goal location with uncrossed hands, shifts of attention related to movement planning may be connected differently to anatomical and external spatial reference frames for head- versus eye-movements. Third, the localization of tactile targets at the proximal versus distal location of the hand (Rorden et al., 2002) may have emphasized external spatial information in comparison to discriminating non-spatial vibrotactile features, as required in the present study. Moreover, the direction of the observed (trend-only) effect is in contrast with the ERP results in Experiment 6.1 (chapter 6.1) and with the study by Gherri and Forster (2012a): somatosensory ERP effects related to movement planning were not significantly modulated by hand posture in either study, indicating that movement planning related effects were encoded predominantly in one reference frame. The present (trend for a) crossing effect may indicate that anatomical and external spatial information were indeed taken into account even though they were not necessary to discriminate tactile stimuli.

6.3 Experiments 6.3a and 6.3b: tactile discrimination at the movement goal and at the effector

One possible explanation for the rather weak effects observed in the Experiment 6.2 is that stimulus locations at the hand did not coincide with the motor end point of the planned pointing movement and were, thus, not directly involved in the movement planning. We followed up on this potential weakness of experiment 6.2 by including tactile stimulations at locations that coincided with the motor end point of a movement: in these new set of experiments, participants received tactile stimulations at their index fingers while they planned to touch their nose with a finger, or to touch a finger with their nose.

In the previous studies only a pointing movement with the nose in the direction of the goal finger had been required. Experiments 6.1 and 6.2 had explored attentional effects at the goal location of planned head movements. However, it is possible that during movement planning tactile attention is shifted not to the goal location, but rather to the movement effector (cf. Forster & Eimer, 2007). Such a general strategy

of attention allocation might be sensible given that most movement goals are not defined tactually, whereas limb movements always produce tactile sensations that may be relevant, for instance, for online movement corrections. Here, we explicitly dissociated these two possibilities by requiring participants either to move the head to touch one index finger (Experiment 6.3a), or to move one index finger to touch the nose (Experiment 6.3b). Index fingers, thus, served either as movement goals (Experiment 6.3a) or as effectors (Experiment 6.3b). Similar to experiments 6.1 and 6.2, the involvement of spatial reference frames in the coding of movement planning related effects was probed by varying the hand posture (uncrossed or crossed).

In each trial, an auditory cue indicated to the participants which index finger was task-relevant to serve as a movement goal (Experiment 6.3a) or as an effector (Experiment 6.3b). We hypothesized that tactile discrimination performance during movement planning would be enhanced at both the movement goal and the effector compared to control locations. In addition, an attenuation of movement planning effects by hand crossing would indicate an involvement of an anatomical and external spatial reference frame in movement planning related attention allocation. In contrast, similar effects across postures would indicate that an anatomical reference frame alone determines attentional shifts related to movement planning.

6.3.1 Methods

Setup and apparatus were identical in experiments 6.3a and 6.3b and are described in the following.

6.3.1.1 Participants

For experiment 6.3a, data of seventeen participants were analyzed (15 female; 15 right handed; mean age: 22.6 years; age range from 19 to 31 years). However, the original number of participants tested was higher ($n = 28$). Data of eleven participants was discarded from analysis: four participants aborted the experiment; seven participants had to be excluded due to technical reasons, that is, the approximation method to estimate individual performance failed to converge (see below).

For experiment 6.3b, data from nineteen participants (13 female, all right-handed, mean age: 24.9 years; age range from 19 to 44 years) were analyzed. Data from three additional participants had to be excluded from analysis: one participant aborted the experiment; two

participants had to be excluded due to technical reasons, that is, the approximation method to estimate individual performance failed to converge (see below). Each participant participated in one of the experiments (6.3a and 6.3b) only.

All participants tested in experiments 6.3a and 6.3b were neurologically healthy by self-report and had normal or corrected-to-normal vision. All participants gave informed written consent and received course credit or monetary reimbursement for their participation (7 Euro/h). The study was approved by the German Psychological Society (TB 122010) and was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki (World Medical Association, 2013).

6.3.1.2 Apparatus

Participants were comfortably seated in a chair, with their elbows resting on a table in front of them. Participants held their hands in front of their face in an uncrossed or a crossed posture, with the index fingers pointing upwards (Fig. 6.6). Participants wore earplugs, headphones and a blindfold during the whole experiment.

Loudspeakers were used to present white noise to mask all sounds elicited by the tactile stimulators. Responses were recorded by means of a foot pedal under the right foot. Movement recording was done with an NDI Optotrak Certus at a frequency of 100 Hz and controlled with the Optotrak Toolbox by V. H. Franz (<http://webapp6.rrz.uni-hamburg.de/allpsy/vf/OptotrakToolbox>) within Matlab (Mathworks, Natick, MA, USA). Optotrak markers were attached to the nose and to the tips of the index fingers.

6.3.1.3 Stimuli

All auditory stimuli were created with the open source software Audacity (<http://audacity.sourceforge.net>) and controlled with Psychtoolbox (Brainard, D. H., 1997, The Psychophysics Toolbox, Spatial Vision 10:433-436) within Matlab (Mathworks, Natick, MA, USA). Custom built vibrotactile stimulators were attached to each index finger at the lateral side of the middle phalanx. The stimulators were driven with a tuning frequency of 100 Hz. Tactile target stimuli consisted of either three or four short pulses, lasting 500 ms in total including gaps between stimulations. The silent gap between pulses was set to 30 ms at the beginning of the experiment. Participants had to discriminate between the three- and four-pulsed stimuli. A longer gap between the

pulses facilitates the discrimination. An adaptive method was used to adjust the gap size to account for individual performance differences. The size of the silent gap between vibrotactile pulses was adapted for each experimental condition (uncrossed vs. crossed hands; tactile stimulus at the cued vs. uncued hand) throughout the whole experiment using a non-parametric accelerated stochastic approximation method (Kesten, 1958; Robbins & Sutton, 1951). The approximation method was used to find the threshold at which the participant would correctly respond in 75 % of the trials. The gap used in the subsequent trial was determined with the following formula:

$$X_{n+1} = X_n - c / (2 + m_{\text{shift}}) * (Z_n - \phi),$$

X_n denotes the gap in trial n , X_{n+1} denotes the gap in the subsequent trial, c denotes a step size constant, which was set to 20 ms.

Z_n denotes the response in trial n (set to 1 for correct responses and to 0 for incorrect responses), m_{shift} denotes the accumulated number of shifts in the response category in all trials (i.e. correct vs. incorrect), and ϕ denotes the detection threshold that was set to 0.75. Thus, the smaller the number of changes in sign before the n th step, the larger the corrections of gap size X_n at the n th step (Kesten, 1958). The gap size resulting from this adaptation procedure was used as the dependent variable for statistical analysis.

6.3.1.4 Procedure

In experiment 6.3a, participants planned and executed a movement with their nose to touch the tip of one of their index fingers (Fig. 6.6). In experiment 6.3b, participants planned and executed a movement with one of their index fingers to touch the tip of their nose. During movement planning, participants received a tactile stimulus at one of their index fingers. After movement execution they had to respond whether the tactile stimulus consisted of three or four pulses.

Each trial started with checking the position of the nose marker along the x -axis (Fig. 6.6A) to make sure that the nose was located approximately in the middle between the index fingers (± 20 mm). If this position check was not successful within 5000 ms, an error sound was presented. If the position check was successful, a movement cue was presented for 100 ms, which consisted of either a pink noise burst or a beep sound (rectangle shaped, 440 Hz). This cue indicated the index

finger (left vs. right) that served as movement goal (experiment 6.3a), and the index finger to be used as an effector (experiment 6.3b), respectively. The cue-finger association was counterbalanced across participants and was independent of hand posture. A tactile target stimulus was randomly presented at one index finger 600 to 900 ms after onset of the auditory cue that indicated the relevant index finger. An auditory go-cue (100 ms, 1000 Hz) was presented after another random interval between 200 to 300 ms following the tactile stimulation offset and instructed the participant to initiate the movement.

The distance between the marker on the nose and the marker on the cued finger was compared online along the x-axis to make sure that the correct finger was touched (experiment 6.3a) or moved (experiment 6.3b), respectively. If the nose marker and the marker of the cued finger were at rest for 500 ms, an auditory cue (100 ms, 1000 Hz) was presented to indicate the completion of the movement. After movement completion, participants responded by means of a foot pedal whether they had perceived three or four tactile pulses (toe lift vs. heel lift). The stimulus-response mapping was counterbalanced across participants. Participants completed eight blocks of 40 trials with half of the blocks in an uncrossed arms posture and half of the blocks in a crossed posture. After every two blocks the arm position was changed. The starting position was randomized across participants.

6.3.1.5 Practice

As practice, participants completed one block of 40 trials of head movements without any tactile stimulation. Then, participants were familiarized with the tactile stimuli and completed at least two additional blocks of 40 trials, one with uncrossed and one with crossed hands, under the same conditions as in the subsequent experiment.

6.3.1.6 Error control during movement execution

Movements were analyzed online. Trials with movement errors were discarded and repeated at a random position during the remaining block. A movement error was defined as a movement onset faster than 100 ms after go cue onset, the lack of movement until 700 ms after go cue onset, a deviation of the finger or nose position by more than 20 mm along the x-axis, when they were to stay still in that trial, and a

movement completion later than 1.5 s after go cue onset, that is, when the difference between the nose marker and the marker of the cued finger was reduced to less than 10 mm along the x-axis. If an error occurred, a feedback sound was played consisting of either a 400 ms long 1000 Hz sine wave ('too fast' movement) or four repeated 100 ms beep sounds (440 Hz) (all other error types).

6.3.1.7 Analysis of gap sizes

The gap size of the last adapted trial was used as estimate for the threshold at which participants responded correctly in 75 %. Whether the adaptive procedure successfully converged was checked via visual inspection by plotting the gap size as a function of the trial number. Convergence failed in 9 participants (7 out of 28 in experiment 6.3a; 2 out of 22 in experiment 6.3b) and these were excluded from analysis. For each experiment, individual estimates of the final gap size were entered in an ANOVA for repeated measures with the within-subject factors Posture (uncrossed vs. crossed) and Hand (cued vs. uncued).

6.3.2 Results

The group averages and individual final gap sizes are plotted in Fig. 6.7. For experiment 6.3a, the ANOVA with factors Posture and Hand revealed a trend for a main effect of Hand, with smaller gap sizes when stimuli were presented at the cued than at the uncued hand ($F(1, 16) = 4.11, p = 0.059$). Posture did not significantly modulate the size of the estimates ($F < 1$) and did not interact with the factor Hand ($F < 1$). For experiment 6.3b, the ANOVA with factors Posture and Hand neither revealed significant effects of Posture or Hand, nor a significant interaction between the two factors (all $F < 1$).

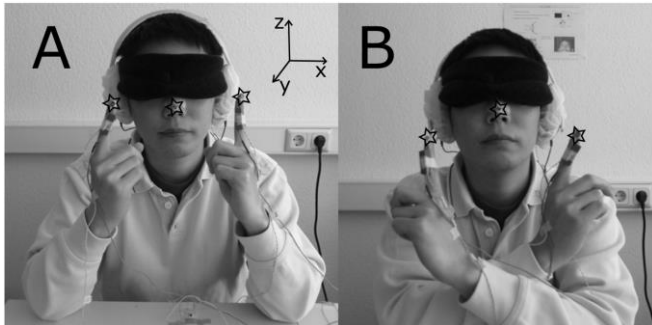


Figure 6.6. Setup of behavioral experiments 6.3a and 6.3b. At the beginning of each trial, participants were cued to plan a movement. The movement consisted of either moving the head to touch the tip of the cued index finger (left vs. right) with the nose (experiment 6.3a) or moving the cued index finger to touch the nose (experiment 6.3b). Following the movement cue, a vibrotactile target stimulus was presented at one of the index fingers. A subsequent auditory go-cue signaled participants to start the movement. Participants executed the cued movement, returned to a central head position, and responded via a foot pedal to the tactile stimulation. The hand posture was either uncrossed (**A**) or crossed (**B**) and was varied in a blockwise fashion. Movements were measured along the x, y, and z-axis (coordinate system depicted in **A**) with LED markers (black stars).

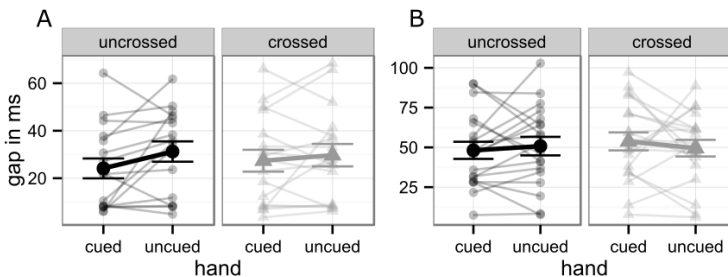


Figure 6.7. Results of Experiments 6.3a (**A**) and 6.3b (**B**). The size of the final gap between vibrotactile stimuli at the end of the experiments is depicted when the cued index finger served as movement goal (**A**; experiment 6.3a), and as effector (**B**; experiment 6.3b). The size of the final gap is shown for tactile stimuli presented at the cued hand (left in each panel) and at the uncued, non-goal hand (right in each panel) with uncrossed (left panels; black circles) and crossed hands (right panels; gray triangles). The group average is depicted with large opaque symbols. Whiskers represent the SEM. Semi-transparent symbols and lines represent individual participant data. Note, scales differ between **A** and **B**.

6.3.3 Experiment 6.3a and 6.3b: Discussion

The two experiments were conducted to investigate behavioral effects of goal-directed movement planning on tactile perception at the movement goal and at the movement effector. In each trial, a cue indicated the finger that served as the movement goal (experiment 6.3a) or effector (experiment 6.3b), respectively. During movement planning, tactile discrimination performance has been reported to be enhanced at the effector finger compared to a non-effector finger for non-goal directed movements (Juravle & Deubel, 2009; van Ede et al., 2015) and at the goal of a saccade to one hand compared to the non-goal hand (Rorden et al., 2002). It was, thus, hypothesized that tactile discrimination performance would be enhanced at the cued compared to the uncued finger during movement planning. In addition, it was hypothesized that hand posture would modulate such movement planning effects if anatomical and external spatial reference frames were involved in planning related shift of tactile attention. However, the present results provide only weak support for these hypotheses: In experiment 6.3a, in which index fingers served as movement goals, there was a trend for enhanced tactile discrimination performance at the cued compared to the uncued finger. Hand posture neither significantly modulated overall performance nor the movement planning effect. In experiment 6.3b, in which one of the index fingers served as the movement effector, tactile discrimination performance was neither significantly modulated by movement planning nor by hand posture.

It is noteworthy, however, that a trend for an effect of movement planning was observed when index fingers served as movement goals only (experiment 6.3a). This (trend for an) effect may indicate that movement planning shifted tactile attention towards the movement goal, but not towards the effector (experiment 6.3b). This notion, however, contrasts with the suggestion that tactile attention is shifted to the effector, and not to the movement goal during the planning of goal-directed manual reaching (Forster & Eimer, 2007). The failure to observe significant effects of movement planning may be due to the large variance between participants, as evident when looking at individual results, in which no systematic pattern is observable (Fig. 6.7). It is possible that this large variance is due to the nature of the algorithm used to determine gap size. Responses at the beginning of the experiment influenced the estimation of the gap size much more than

responses later in the course of the experiment (cf. Kesten, 1958), implying that inter-individual learning effects or strategy changes at later points in time of the experiment are reflected in the data to little extent only. Thus, despite all participants having practiced the task before the experiment, part of the variance may be due to inter-individual differences in how fast participants learned to perform the task. Alternatively, the link between movement planning of an effector other than the eye and covert spatial attention may be weaker than the tight link between the saccadic system and covert spatial attention, as suggested in previous literature.

In sum, based on the present two experiments it is still unclear whether goal-directed movement planning with an effector other than the eye enhances tactile perception at a movement-relevant location, such as at the effector or at the movement goal.

6.4 General discussion

Four experiments were conducted to assess effects of movement planning on tactile processing. Based on the claim of the *premotor theory of attention* that movement planning and covert spatial attention are controlled by the same neural mechanisms (Rizzolatti et al., 1994), it was hypothesized that movement planning leads to a shift of tactile spatial attention towards the movement goal. However, the present result pattern yields, if only, weak evidence to support this hypothesis: First, the result pattern and the timing of effects on somatosensory ERPs (Experiment 6.1) contrast previous studies, reporting covert spatial attention effects on somatosensory ERPs (Eardley & van Velzen, 2011; Eimer et al., 2003; Heed & Röder, 2010; Michie et al., 1987; Röder et al., 2008; Zopf, Giabbiconi, Gruber, & Müller, 2004), and studies reporting effects of non-goal-directed movement planning (Eimer et al., 2005; Gherri & Forster, 2012a, 2012b). Second, only a trend for a significant movement planning effect on tactile discrimination performance was observed (Experiments 6.2, 6.3a), indicating that the evidence for an effect was rather weak. It is possible that tactile attention is shifted not to the goal location, but rather to the executing effector (cf. Forster & Eimer, 2007). Given that most movement goals are not defined tactually such a strategy might be useful, because limb movements always produce tactile sensations that may be relevant for online movement corrections. Yet, this hypothesis could not be confirmed as tactile discrimination performance did not significantly differ at the effector and at the non-effector hand in preparation of a movement (Experiment 6.3b). Thus, movement planning did not appear to shift tactile attention to the movement goal or to the effector.

The involvement of anatomical and external spatial reference frames in the coding of movement planning related effects was probed in all experiments by crossing the hands over the midline. Yet, hand crossing did not significantly modulate movement planning effects. This observation could be due to at least two reasons. First, effects of movement planning were weak, if present at all, thus making a further modulation by hand posture difficult to observe. Second, attentional shifts related to movement planning of a body part and covert tactile attention may be connected to spatial reference frames via different mechanisms (Gherri & Forster, 2012a) and it is, thus, possible that hypothesized effects related to movement planning and spatial reference frames are not present at all. Whereas effects of covert

spatial attention on somatosensory ERPs have been observed to be modulated by hand posture (Eardley & van Velzen, 2011; Eimer et al., 2003; Heed & Röder, 2010; Röder et al., 2008), effects related to movement planning on somatosensory ERPs in the present (Experiment 6.1) and in previous studies have not been significantly modulated by hand posture (Gherri & Forster, 2012a, 2012b). In addition, hand posture did not significantly modulate effects of movement planning on tactile discrimination performance (Experiment 6.2, 6.3a and 6.3b). The differential modulation of effects by hand posture between paradigms investigating movement planning and paradigms investigating covert tactile attention indicates that covert tactile attention and movement planning may not be guided by common neural mechanisms. Together with the present observation that movement planning did not appear to lead to a shift of tactile attention, this is in direct contrast to the premotor theory of attention (Rizzolatti et al., 1994). One may argue instead for two separate, but closely linked mechanisms for covert attention and motor planning (cf. Ley & Röder, 2014).

However, it remains unclear why movement planning effects observed in other studies did not appear to generalize to the present experimental setting. Possibly, the visual system modulates how motor planning and spatial attentional mechanisms interact. In fact, the premotor theory of attention was based on visual research, assuming that spatial attention and saccade control systems are guided by the same neural mechanisms (Corbetta, 1998; Nobre et al., 2000; Rizzolatti et al., 1987, 1994). In the same vein, planning a saccade reportedly enhances sensory processing at the movement goal compared to a control location (Baldauf & Deubel, 2008b; Collins & Doré-Mazars, 2006; Collins et al., 2010; Deubel & Schneider, 1996; Jonikaitis et al., 2011; Juravle & Deubel, 2009; Rolfs et al., 2011; Rorden & Driver, 1999; Rorden et al., 2002). Moreover, visual discrimination performance has been reported to be enhanced at the movement goal compared to control locations for goal-directed manual movements (Baldauf et al., 2006; Collins et al., 2008; Deubel & Schneider, 2004; Deubel et al., 1998; Rolfs et al., 2013; Schiegg et al., 2003). However, evidence, which shows that goal-directed movement planning with effectors other than the eyes influences sensory processing in a modality other than vision, is scarce. There is some evidence showing that planning of non-goal directed movements enhances tactile discrimination performance (Juravle & Deubel, 2009; van Ede et al., 2015) and somatosensory ERPs

elicited by tactile stimuli (Eimer et al., 2005; Gherri & Forster, 2012a, 2012b) at the effector hand compared to the other, resting hand. However, in all these studies participants had their eyes open, whereas in the present experiments participants were blindfolded. Given that movement planning in the present experiments could not be reliably associated with a shift of tactile attention, it is, thus, possible that visual information about the effector location contributes to interactions between spatial attention and movement planning. This may be a sensible strategy as people frequently look at the moving effector when executing hand movements. Moreover, the underlying mechanisms of covert tactile spatial attention have been reported to critically depend on developmental vision (cf. Chapters 3 & 4; Eardley & van Velzen, 2011; Forster et al., 2007; Röder et al., 2008; Schubert et al., 2015), highlighting the role of the visual system on spatial attentional processing. Thus, the visual system may play a pivotal role in the interactions between spatial attention and movement planning.

Alternatively, the present paradigms may not have been sensitive to uncover the rather weak link between head movement planning and tactile attention. We observed a relatively high number of participants whose data were discarded from analysis, because they failed to perform movements properly, were not able to follow response instructions, or responded at chance level in the tactile discrimination task. This observation may relate to the fact that the head is infrequently used as a sole effector to interact with the world. An infrequent use, in turn, may have increased overall task difficulty, precluding an observation of hypothesized effects.

6.5 Conclusion

The premotor theory of attention claims that movement planning shifts spatial attention to the spatial location of the movement goal. The present observations do not give strong support to this claim. In the present experiments goal-directed movement planning with the head and the hands did not appear to shift tactile attention either to the movement goal or to the effector. Effects of movement planning have been frequently observed for eye movements on visual, tactile, and auditory stimulus processing and for manual movements on visual stimulus processing. Yet, such effects of movement planning may not trivially generalize from the saccadic system to all effectors and all modalities.

Chapter 7: Discussion

At every moment in time we are exposed to a myriad of signals arriving at multiple sensory channels. Despite this seemingly chaotic sensory mélange, our brain manages to construct a coherent percept of the world. Studying the influence of multimodal information on tactile processing, as in the present thesis, offers one way to investigate how the brain integrates such multisensory information. The main findings of the presented studies will be summarized in the following, and subsequently discussed.

In the **first study**, I addressed the question of how the encoding of tactile spatial information is reflected in neural oscillatory activity in sighted and congenitally blind individuals (Chapters 3 & 4). Tactile spatial encoding is known to differ between these populations. Posterior parietal alpha-band activity was identified to be a neural correlate of why sighted and congenitally blind individuals differentially encode tactile spatial information. The electroencephalogram (EEG) of sighted and congenitally blind participants was recorded while they were cued to attend to one hand to detect rare tactile target stimuli at that hand and to ignore target stimuli at the other hand as well as frequent standard stimuli to either hand. The location of a tactile stimulus can be represented relative to an anatomical skin-based reference frame and relative to a posture-related external spatial reference frame. To probe tactile spatial reference frames participants held their hands either in an uncrossed or in a crossed posture (cf. Fig. 2.1). Critically, spatial reference frames were misaligned with crossed hands, that is, the left hand occupied the right external space and vice versa. During attentional orienting (Chapter 3), hand crossing selectively attenuated the lateralization of sighted participants' posterior parietal alpha-band activity, suggesting an influence of external spatial information on activity associated with attentional orienting. Similarly, during tactile stimulus processing (Chapter 4) hand crossing selectively attenuated attention-related alpha-band suppression predominantly over ipsilateral posterior parietal cortex. In contrast to the sighted, oscillatory activity was not significantly affected by hand posture in congenitally blind individuals neither during attentional orienting (Chapter 3) nor during tactile stimulus processing (Chapter 4).

Moreover, central alpha-band activity as well as central and parietal beta-band activity was associated with coding of anatomical spatial information in both sighted and blind individuals. Specifically, lateralization of central alpha-band activity as well as central and

parietal beta-band activity during attentional orienting (Chapter 3) and attention-related modulations of these frequency bands following tactile stimulation were not modulated by hand posture in either group (Chapter 4). During stimulus processing, an ipsilateral suppression of central alpha as well as beta-band activity in sighted and a contralateral alpha- and beta-band enhancement in blind individuals (Chapter 4) were associated with attention, that is, comparing activity elicited by attended versus unattended stimuli, but were not significantly modulated by hand posture.

Together, the observation that alpha-band activity related to external spatial coordinates is in line with the association between eye-centered external spatial coding of touch and posterior parietal alpha-band oscillations in sighted individuals in the context of movement planning to remembered tactile targets (Buchholz et al., 2011, 2013). Additionally, the present study adds to previous work that identified developmental vision to be critically involved in how skin-based anatomical and posture-related external spatial information is integrated. Whereas normally sighted humans automatically integrate anatomical and external spatial information (Shore et al., 2002; Yamamoto & Kitazawa, 2001), it had been suggested that congenitally blind individuals do not integrate external spatial information for tactile localization by default (Collignon et al., 2009; Röder et al., 2008, 2004). Because the generative neural mechanisms for posterior alpha-band activity seem to be linked to developmental vision (cf. R. J. Berger et al., 1962; Birbaumer, 1971; Krieger et al., 2006; Novikova, 1973), the reduction of this neural mechanism in congenitally blind individuals may be related to their preferred use of anatomical over external spatial codes for tactile processing.

The differential encoding of spatial information of touch as observed in the **first study** may be explained in two ways: first, congenitally blind may not integrate anatomical and external spatial codes for touch.

Second, congenitally blind individuals may remap touch into external space, integrate anatomical and external spatial information, but use different default integration weights than sighted individuals. The **second study** (Chapter 5) sought to differentiate between these possibilities by testing whether certain task demands would trigger the integration of external and anatomical spatial information for touch in congenitally blind individuals. According to the first explanation task context should not affect blind participants' tactile localization

performance. In contrast, blind participants' tactile localization should be affected by task context according to the latter explanation. Sighted and congenitally blind participants localized tactile target stimuli presented to the palm or back of either hand while ignoring tactile distractor stimuli presented to the opposite hand. Critically, participants reported either the anatomical ("palm" or "back" of the hand) or the external spatial location of the target stimulus ("up" or "down" in space). Varying the orientation of the hands allowed to test whether congruency effects, that is, better performance for congruent than incongruent target-distractor pairs, were determined by anatomical or by external spatial locations. Under anatomical instructions, performance was better for target-distractor pairs presented to anatomically congruent than incongruent locations. In contrast, under external instructions, performance was best for target-distractor pairs presented to locations congruent in external space. These congruency effect modulations were comparable in sighted and blind participants, even if effects were smaller in the latter group. The results suggest that blind individuals, like sighted persons, remap anatomical information into external space and integrate anatomical and external information during tactile localization with flexibly adjusted integration weights.

The **second study** of the present thesis (Chapter 5) substantiates previous findings in sighted adults showing that task demands, such as instructions and the context of movements, modulate tactile localization (e.g., Azañón et al., 2015; Badde, Heed, et al., 2015; Badde, Röder, et al., 2015; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012), presumably due to weight adjustments for the spatial integration of skin-based and external, posture-based information (Badde & Heed, in press).

Moreover, it challenges the view that congenitally blind humans relied exclusively on skin-based information when localizing touch and, thus, refrain from automatic integration of external spatial codes (Collignon et al., 2009; Röder et al., 2008, 2004) by showing that congenitally blind individuals do integrate external spatial information, at least under some task demands. Furthermore, it is in line with recent studies in congenitally blind individuals suggesting an integration of external spatial codes for tactile localization in the context of bimanual movements (Heed, Möller, et al., 2015) and in the context of task instructions asking for a localization of touch relative to external space (Badde et al., 2016). Finally, it fits well with studies in congenitally and

early blind individuals showing an integration of external spatial codes that is similar to that of sighted individuals for synchronized bimanual movements (Heed & Röder, 2014), for sequential motor learning (Crollen et al., 2013), and for the mental representation of time (Bottini et al., 2015). In sum, the integration of anatomical and external spatial information in tactile processing appears to be flexible and strategic even in the absence of developmental vision.

The **third study** (Chapter 6) investigated the question of whether the planning of goal-directed head and hand movements would shift tactile spatial attention, that is, an enhancement of tactile processing, to one hand when it served as a movement goal and as a movement effector. Moreover, the study asked whether effects on tactile processing related to movement planning would operate according to an anatomical or to an external spatial reference frame. In three paradigms, participants planned and executed pointing and reaching movements with the head and with the hands. During movement planning, a tactile stimulus was presented to either hand and EEG activity as well as discrimination performance in response to tactile stimulation was recorded. I hypothesized that the planning of a pointing movement with the nose would enhance tactile stimulus processing at the hand that served as a movement goal (Experiments 6.1, 6.2, 6.3a). Moreover, I tested how planning of a manual movement modulated tactile processing at the effector hand when reaching with one hand to the nose (Experiment 3b).

In order to test whether anatomical and external spatial reference frames modulated these effects hands were either in an uncrossed or in a crossed hands posture in all paradigms. Yet, the findings did not lend strong support to the hypothesis that movement planning shifts spatial attention towards the movement goal. Specifically, the result pattern and the timing of effects on somatosensory ERPs (Experiment 6.1) contrasted with previous studies, reporting covert spatial attention effects on somatosensory ERPs (Eimer & Forster, 2003; Heed & Röder, 2010; Michie et al., 1987; Röder et al., 2008; Zopf et al., 2004), and studies reporting effects of non-goal-directed movement planning on somatosensory ERPs (Eimer et al., 2005; Gherri & Forster, 2012a, 2012b). Second, only a trend for a significant movement planning effect on tactile discrimination performance was observed at the goal compared to the non-goal hand (Experiments 6.2, 6.3a), indicating that the evidence for an effect was rather weak. Similarly, no significant

difference was observed for tactile discrimination performance at the effector hand compared to non-effector hand (Experiment 6.3b). Furthermore, misalignment of spatial reference frames by means of hand crossing did not significantly modulate movement related effects, presumably because no significant effects of movement planning on tactile processing were observed that could be related to shifts of spatial attention.

The results of the **third study** (Chapter 6) contrast with the premotor theory of attention, which proposes that movement planning and covert shifts of spatial attention are governed by the same neural mechanisms (Corbetta et al., 1998; Nobre et al., 2000; Rizzolatti et al., 1994). One of the claims of this theory is that movement planning shifts spatial attention towards the movement goal, resulting in enhanced sensory processing (Rizzolatti et al., 1994). In support of this claim is that visual, auditory, and tactile processing are enhanced during the planning of a saccade at the movement goal (e.g. Deubel & Schneider, 1996; Rolfs et al., 2011; Rorden & Driver, 1999; Rorden et al., 2002). Similarly, visual processing has been reported to be enhanced at the goal of a planned hand movement (Baldauf et al., 2006).

Yet, evidence linking shifts of tactile attention to the planning of goal-directed movements with an effector other than the eyes is scarce. The present study aimed to fill this gap (Chapter 6). However, in the present study, goal-directed movement planning with the head and the hands appeared to shift tactile attention neither to the movement goal nor to the effector, respectively. Several possibilities may explain these results. The applied paradigms may not have been sensitive to uncover the rather weak link between head movement planning and tactile attention. The head is infrequently used as a sole effector to interact with the environment. An infrequent use may have increased the difficulty of the employed task, consisting of the head movement and the tactile discrimination. Such an increased difficulty may be reflected in the high number of participants who were not included in the data analysis, because they failed to perform the movement properly, were not able to follow response instructions, or gave responses at chance level (Experiments 6.2 & 6.3). Moreover, one may speculate that head movements are somewhat less precise than saccades or hand movements. Planning a head movement to one side may then shift spatial attention rather to a broad area than to a specific location. Finally, the link between attentional mechanisms and movement

planning may predominantly depend on the visual system. Effects of goal-directed movement planning have been observed during the preparation of saccadic eye movement for visual, tactile, and auditory stimulus processing and during the preparation of manual movements for visual stimulus processing (e.g. Baldauf et al., 2006; Deubel & Schneider, 1996; Juravle & Deubel, 2009; Rolfs et al., 2011; Rorden & Driver, 1999; Rorden et al., 2002). Additionally, effects of non-goal directed movement planning on tactile processing have been reported only when visual information was available, blindfolded participants were not tested (Eimer et al., 2005; Forster & Eimer, 2007; Gherri & Forster, 2012a, 2012b; Juravle & Deubel, 2009; van Ede et al., 2015). Thus, when linking movement planning and spatial attentional mechanisms the visual system was either directly involved by employing the eyes as an effector and/or sensory organ, or indirectly by the availability of task-unrelated visual information.

In conclusion, contrary to the tight link between the visual system and spatial attentional mechanisms, the relation between tactile spatial attention and goal-directed movement planning with the head and hand appears to be rather weak. This may indicate that the link between movement planning and spatial attention does not hold for all effectors and all sensory modalities.

Oscillatory brain activity and the spatial encoding of touch

The present modulations of oscillatory alpha- and beta-band activity in sighted individuals suggest a concurrent encoding of spatial reference frames in distributed and overlapping brain regions (Chapters 3 & 4). To localize touch the brain must transform and integrate information coming from multiple senses, involving the necessity to transfer information across brain regions. Oscillations in the alpha- and beta-band range may provide a mechanism that allows the brain to orchestrate information transfer between sensorimotor and parietal areas and to implement the largely automatic integration of original and transformed spatial information for touch (cf. Heed, Buchholz, et al., 2015). Oscillatory brain activity is well suited to synchronize intra- and interregional neuronal activity as dynamic changes of the synchronized activity pattern can flexibly alter the brain's communication at multiple spatial and temporal scales (Engel et al., 2013; Fries, 2005, 2015). Flexible changes of the brain's communication allow the brain to adapt to specific contextual information that may be driven in a top-down

fashion by internal sources or in a bottom-up fashion by external sources (Fries, 2015; Siegel et al., 2012). Moreover, one area may be involved in several functional networks and carry several types of information that are encoded in different frequency bands (Akam & Kullmann, 2014; Siegel et al., 2012). For tactile localization, this would allow a concurrent encoding of anatomical and external spatial information (Heed, Buchholz, et al., 2015). Such a parallel representation of spatial reference frames has been suggested to be implemented by a distributed neural code that allows a flexible location estimate by integrating original and transformed sensory representations (Heed, Buchholz, et al., 2015).

Flexible weighting of spatial tactile information in both presence and absence of developmental vision

In the present thesis, the integration of anatomical and external spatial information for tactile localization depended on current task instructions in both sighted and congenitally blind individuals (Chapter 5). It may be the use of different default integration weights, possibly biased strongly towards anatomical, skin-based coordinates, that produced previously observed differences in touch localization between sighted and congenitally blind individuals (cf. Ley, 2015). In this view, the differences in alpha-band activity between sighted and congenitally blind individuals found in the thesis' studies for the encoding of external spatial information (Chapters 3 & 4) would reflect such altered weighting of external spatial information in congenitally blind individuals. A recent study provides a hint that posterior-parietal alpha-band lateralization may reflect individual weighting of external eye-centered information for visual localization in the context of passive whole body motion, which requires an updating of visual space. Gutteling, Selen, and Medendorp (2015) investigated the individual performance to correctly update the spatial location of a remembered visual target stimulus relative to eye-fixation following passive whole body motion. This performance correlated with the modulation strength of posterior parietal alpha-band lateralization related to the remapping of visual space, that is, activity before and after passive whole body motion (Gutteling et al., 2015). In addition, Tramper and Medendorp (2015) recently showed that the location of a remembered visual stimulus presented shortly before passive whole body motion is updated relative to both an eye-centered and an body-centered

reference frame following passive whole body motion. They suggested that both reference frames are encoded in parallel, weighted according to their reliability, and integrated to an optimal location estimate of the remembered visual stimulus following passive whole body motion (Tramper & Medendorp, 2015). Alpha-band lateralization could, thus, reflect the weighted integration of information coming from an external eye-centered and an external body-centered reference frame.

Whether alpha-band lateralization reflects the weighted integration of anatomical and external spatial coordinates in the tactile modality could be tested by correlating individual weights assigned to anatomical and external spatial information for touch (cf. Badde, Heed, et al., 2015) with individual alpha-band lateralization in normally sighted individuals. Moreover, the weights for the integration of anatomical and external tactile information do not appear to be rigid, neither in the presence (Badde, Heed, et al., 2015; Badde, Röder, et al., 2015; Gallace et al., 2008; Mueller & Fiehler, 2014a, 2014a; Pritchett et al., 2012) nor in the absence of developmental vision (Chapter 5; Badde et al., 2016; Heed, Möller, et al., 2015). An altered weighting of spatial information by current task demands should be expressed in oscillatory power modulations and in dynamic changes of within and inter-area coupling of oscillatory networks in both sighted and congenitally blind individuals.

Outlook: Developmental aspects of oscillatory activity

Closely related to the differences between sighted and congenitally blind individuals in the implementation of oscillatory alpha-band activity (Chapters 3 & 4) is the question of how alpha-band activity develops during ontogeny. Consistent with previous findings (R. J. Berger et al., 1962; Birbaumer, 1971; Kriegseis et al., 2006; Novikova, 1973), a reduced posterior parietal alpha-band rhythm was observed in congenitally blind compared to sighted individuals in the present thesis (Chapter 3). Similarly, alpha-band activity is reduced in bilateral congenital dense cataract patients who regained vision later in life, suggesting that alpha-band activity develops under the critical influence especially of early visual experiences (Bottari et al., 2016). In typically developing individuals, oscillatory activity markedly changes from early infancy until late adolescence, evident in frequency and amplitude modulations (Başar, 2012; Lindsley, 1939) as well as in altered functional and directed connectivity patterns within different oscillatory networks

(Michels et al., 2013). For instance, in typically developing children, the average peak frequency of the rhythm, which dominates the occipital EEG signal, that is, the alpha-rhythm, increases with age from 4 Hz at the age of one month to approximately 10 Hz at an age of twelve years (Lindsley, 1939). The amplitude of this dominant rhythm is not observed to be equivalent to that of adults before the age of sixteen years (Lindsley, 1939). The protracted development of the brain's oscillations and connectivity pattern (Lindsley, 1939; Michels et al., 2013) may go hand in hand with the development of multi-sensory processing, that is thought to be immature at birth and to critically depend on early sensory experiences (Burr & Gori, 2012; Knudsen & Knudsen, 1990; Stein, 2012a). Yet, the exact relation between the development of the human brain's oscillations and the development of multisensory processes is largely unknown. Regarding the development of tactile localization, the ability to localize touch in external space begins early, presumably during the first year of life (Begum Ali, Spence, & Bremner, 2015; Bremner, Mareschal, Lloyd-Fox, & Spence, 2008; Rigato, Begum Ali, van Velzen, & Bremner, 2014), and continues to improve during the first years of life (Begum Ali, Cowie, & Bremner, 2014). Yet, an automatic integration of anatomical and external spatial information is not observed before the age of 5.5 years, as evident in hand posture effects on tactile TOJ in children older than 5.5 years, but not in younger children (Pagel et al., 2009). Therefore, the default integration of anatomical and external spatial information should be reflected in oscillatory activity starting around the age of 5.5 years, even though an influence of external spatial coordinates may be evident even earlier in life (see Rigato et al., 2014). However, the oscillatory pattern would not necessarily have to resemble that observed in sighted adults (cf. Chapters 3 & 4; Buchholz et al., 2011, 2013), as the specific relations between oscillations and perception may change over time. For instance, children aged 7 to 10 years have been shown to exhibit an adult-like lateralization of posterior parietal alpha-band activity (8-12 Hz) when cued to direct visual spatial attention to one hemifield (Vollebregt et al., 2015). Yet, the relation between this alpha-band lateralization and visual spatial cueing effects differed in the children compared to previous reports in adults (ter Huurne et al., 2013; Vollebregt et al., 2015).

Specifically, posterior alpha-band lateralization in children was predictive for reaction times in invalidly cued trials rather than for the

cueing benefit as in adults (ter Huurne et al., 2013; Vollebregt et al., 2015). It is, thus, likely that the automated use of anatomical and external spatial information is reflected in the brain's oscillatory activity starting at the age of 5.5 years, but that the pattern of oscillatory activity and the relation between brain oscillations and behavior will not resemble that of adults until a later point during ontogeny. This relation could be investigated by testing children of different age groups using an child-appropriate version of a tactile attention task that probes tactile reference frames by varying the hand posture (see Chapter 3 & 4; Eimer et al., 2003; Pagel et al., 2009; Röder et al., 2008). Such a paradigm should furthermore be designed in a manner that allows the assessment of single trial responses, a prerequisite to directly relate oscillatory activity to behavior (cf. Haegens et al., 2011, 2012; van Ede et al., 2011). Given that tactile attention involves the integration of multisensory information, investigating the brain's oscillations in children during a tactile attention task would provide insight into the development of the underlying neural mechanisms that contribute to multisensory processing.

Outlook: Alpha-band activity reflects an external spatial reference frame, but which one?

In the present thesis, posterior-parietal alpha-band activity was associated with the encoding of information relative to an external spatial reference frame for touch (Chapters 3 & 4). Yet, the question remains open what type of external spatial reference frame had been probed in our study. The present studies did not test the body part to which the external reference frame was anchored, such as the eyes, head, body, or hand. To investigate this issue, hand crossing would have to be manipulated with respect to each of the potential anchors separately (see Heed et al., submitted).

Vision provides the highest spatial resolution compared with the tactile and the auditory modality. Therefore, a representation of environmental multisensory events relative to an eye-centered reference may be advantageous to guide subsequent saccades and limb movements. Several findings support the idea that posterior parietal alpha-band activity reflects tactile coding relative to an eye-centered reference frame. First, posterior parietal alpha-band activity has been reported to reflect the remembered location of visual (Gutteling et al., 2015; Van Der Werf et al., 2013) and tactile targets (Buchholz et al.,

2011, 2013) relative to an eye-centered reference frame. Second, eye position influences the encoding of touch. For instance, tactile localization is biased towards the gaze position (Harrar & Harris, 2009). In addition, directing the eyes to an eccentric position compared to a central position reportedly attenuates the size of attention-related effects on somatosensory ERPs between 200 and 260 ms poststimulus (Gherri & Forster, 2014). Third, in the present thesis hand posture did not significantly modulate posterior-parietal alpha-band activity during attentional orienting and tactile processing in congenitally blind individuals (Chapter 3 & 4), who obviously do not encode space relative to eye position.

Alternatively, posterior parietal alpha-band activity could reflect tactile spatial coding relative to a limb-centered reference frame. Single-cell recordings in the primate brain suggest that multiple reference frames exist that are not only anchored to the eyes, but also to different body-parts (Batista, Buneo, Snyder, & Andersen, 1999; Chen et al., 2013; Graziano & Gross, 1998). In addition, spatial extinction effects on tactile stimuli in neglect patients have been reported to depend on the relative position of the hands rather than on the relative position to the eyes, suggesting a hand-centered coding (Aglioti, Smania, & Peru, 1999). Reference frames centered on the hands or even to individual fingers (Heed, Backhaus, & Röder, 2012) may account for modulations of posterior-parietal alpha-band activity both during attentional orienting to uncrossed and crossed hands and during tactile processing (Chapters 3 and 4; Schubert et al., 2015). Such body part centered reference frames may also account for previous findings suggesting that posterior-parietal alpha-band activity reflects gaze-centered encoding during movement planning to remembered tactile targets (Buchholz et al., 2011, 2013). In the latter studies, participants fixated the ring finger of one hand while tactile targets were presented to the index and little finger of that hand.

In this manner, the locations of the stimulated fingers coincided with the space left and right relative to the gaze direction and, thus, both an eye-centered as well as finger-centered reference frames could account for the observed results. Finally, a recent study aimed at disentangling external spatial reference frames by manipulating the relative positions between hands, eyes, and trunk employing a tactile TOJ task (Heed et al., submitted). Hands were either placed in an uncrossed or crossed posture in different sides of space relative to the eyes and trunk or they

were placed in the same side of space relative to the eyes and the trunk (for an example of some of their manipulations see Fig. 2.1). TOJ hand crossing effects were reduced with both hands placed in the same side of space relative to eye position, indicating an influence of an external eye-centered reference frame. Similarly, yet to a lesser extent, TOJ crossing effects were modulated by the relative position to the trunk. However, eye- and trunk-centered coding did not explain the total size of crossing effects, supporting the suggestion that tactile localization relies on additional, presumably limb-centered reference frames (Heed et al., submitted). Tactile spatial coding appears, thus, to depend on both an eye-centered and a limb-centered reference frame. Measuring the EEG, for instance, during a tactile attention task (Chapters 3 & 4), while separately manipulating eye, head, torso, and hand position (cf. Fig. 2.1) would allow studying the extent to which posterior parietal alpha-band activity reflects the encoding of touch relative to an eye-, head-, torso-, and limb-centered spatial reference frames. Posterior-parietal alpha-band activity may be involved in the weighted integration of external spatial reference frames (cf. Tramper & Medendorp, 2015). It is, thus, likely that each external spatial reference frame modulates oscillatory activity in posterior parietal cortex.

Conclusions

In sum, the findings of the present thesis identified the following factors and mechanisms to be involved in tactile spatial encoding. First, posterior parietal alpha-band activity reflects the coding of external spatial information during both the orienting of tactile attention (Chapter 3) and tactile stimulus processing (Chapter 4), whereas central alpha-band activity as well as beta-band activity reflects encoding relative to an anatomical reference frame. Second, visual experience during ontogeny is critical to set up the generating mechanism for posterior parietal alpha-band oscillations (Chapter 3 & 4). Posterior parietal alpha-band activity, in turn, may be the neural correlate of the differential weighting of external spatial information of touch in sighted and congenitally blind individuals. Third, even though developmental vision appears to be critical for the weighting of anatomical and external spatial information for tactile localization, the weighting of spatial information can be flexibly modulated by task demands under top-down control in the presence and in the absence of developmental vision (Chapter 5). Fourth, goal-directed movement planning has frequently been reported to lead to a shift of spatial attention, evident in enhanced sensory processing of visual, tactile, and auditory stimuli at the movement goal of a planned saccade or in enhanced processing of visual stimuli at the movement goal of a planned manual movement (e.g. Baldauf et al., 2006; Deubel & Schneider, 1996; Rorden & Driver, 1999; Rorden et al., 2002). Here, planning of a goal-directed movement with an effector other than the eye, that is, with the head, did not appear to result in a shift of tactile spatial attention. Thus, the tight link between goal-directed movements and shifts of spatial attention may be specific to the visual system.

In conclusion, the present thesis adds to our understanding of how the brain integrates the multitude of sensory signals it is exposed to at every moment. Both sensory experiences during ontogeny and current task demands influence the integration of the available sensory information. Oscillatory brain activity appears to be one of the underlying neural mechanisms allowing the brain to orchestrate this integration in a flexible fashion. We benefit from such a flexible integration when our brain constructs a coherent percept of the permanently changing world that surrounds us.

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