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Processing and Integration of Sensory Information in Spatial Navigation

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Caspar Mathias Goeke

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Supervisors

1st Supervisor: **Prof. Dr. Peter König**
University of Osnabrück, Osnabrück, Germany

2nd Supervisor: **Prof. Dr. Klaus Gramann**
Technical University of Berlin, Berlin, Germany

3rd Supervisor: **Prof. Dr. Bernhard Riecke**
Simon Fraser University, Vancouver, Canada

Additional Supervisor: **Prof. Dr. Gordon Pipa**
University of Osnabrück, Osnabrück, Germany

Curriculum Vitae

Caspar Goeke

Schepelerstr. 21,
49074 Osnabrück
Germany

cgoeke@uni-osnabrueck.de
+49 157 5521 5307

Journal Articles

Goeke, C., König, S. U., Meilinger, T., & König, P. (submitted). Are non-egocentric spatial reference frames compatible with enacted theories? *Scientific Reports*

König, S. U., Schumann, F., Keyser, J., Goeke, C., Krause, C., Wache, S., … Peter, K. (in press). Learning New Sensorimotor Contingencies: Effects of Long-term Use of Sensory Augmentation on the Brain and Conscious Perception. *PloS One.*

Goeke, C. M., Planera, S., Finger, H., & König, P. (2016). Bayesian Alternation during Tactile Augmentation. *Frontiers in Behavioral Neuroscience*, *10*, 187.

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Conference Contributions

A Bayesian Approach to Multimodal Integration between Augmented and Innate Sensory Modalities, Osnabrück Computational Cognition Alliance Meeting, Osnabrück, Germany 2014

Cultural impact on strategy selection mechanisms, Annual Meeting of Experimental Psychologists, Gießen, Germany, 2014.

Individual Differences in Spatial Navigation, German Annual Neuroscience

Meeting, Göttingen, 2013.

Investigating Reference Frame Proclivities in a virtual Navigation Task, Osnabrück Computational Cognition Alliance Meeting, Osnabrück, Germany 2012.

Properties and Mechanisms of Sensory Enhancement, Proceedings of KogWis, Bamberg, Germany 2012.

Top-down but not bottom-up visual attention is mediated by parietal cortical areas during natural viewing, European Conference of Eye Movements, Marseille, France, 2011.

Supervised B.Sc. and M.Sc. Theses

2016, Greta Häberle (B.Sc.): Neural correlates of multimodal sensory integration between an innate and an augmented sensory modality

2015, Serena Planera (M.Sc.): A Bayesian Approach to Multimodal Integration between an Innate and an Augmented Sensory Modality

2014, Antonia Kaiser (B.Sc.): Alignment - A mental feature of object representation?

2013, Ann-Kristin Meyer (B.Sc.): Influences of body position, motion and vibrotactile information on the performance in a triangle completion task.

2013, Claudia Heller (B.Sc.): Changes in navigation performance in a virtual triangle completion task under altered body positions, motion, and vibrotactile information.

2013, Doreen Jakob (B.Sc.): Development of Reference Frame Use across Age and Gender.

Teaching

SS2016 Action & Cognition II Seminar

WS2016 Action & Cognition I Seminar

SS2015 Action & Cognition II Seminar

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Abstract

As nomads, humanity constantly moved and relocated for hundred thousands of years. Thereby, individuals or small groups of people had to navigate over very long distances in order to survive. As a result, successful spatial navigation was one of the key cognitive abilities, which ensured our survival. Although navigation has nowadays become less life-threatening, exploring our environment and efficiently navigating between places are still very important aspects in our everyday life. However, in order to be able to navigate efficiently, our brain has to perform a series of spatial cognitive operations. This dissertation is structured into three sections, which explore these cognitive operations from three different perspectives.

In the first section I will elaborate about the role of reference frames in human spatial navigation. Specifically, in an online navigation study (study one) I will show that humans have distinct but stable reference frame proclivities. Furthermore, this study demonstrates the existence of a spatial strategy, in which the preference to use a particular reference frame is dependent on the axis of rotation (horizontal vs. vertical). In a follow-up study (study two) I will then analyze the factors underlying performance differences in navigation, as well as individual preferences using one or another spatial strategy. Interestingly, the results suggest that performance measures (reaction time and error rate) are influenced mostly by the factors gender and age. However, even more importantly, I will show that the prevalent factor, which influences the choice for an individual navigation strategy, is the cultural background of the participant. This underlines the importance of socio-economic aspects in human spatial navigation. In the second part of this thesis I will then discuss aspects of learning and memorizing spatial information. In this respect, the alignment study (study three) will show that humans are able to recall object-to-object relations (e.g. how to get from A to B) in a very brief time, indicating that such information is directly stored in memory. This supports an embodied (action-oriented) perspective of human spatial cognition. Following this approach, in the feelSpace study (study four) I will then investigate the long-term training effects with a sensory augmentation device. Most importantly, the respective results will demonstrate substantial changes in the subjective perception of space, in sleep stage architecture, and in neural oscillations during sleep. In the third and last section I will describe the importance of

multimodal processes in spatial cognitive operations. Most importantly, in the platform study (study five) I will combine the topics of sensory augmentation and Bayesian cue combination. The results of this study show that untrained adult participants alternate rather than integrate between augmented and native sensory information. Interestingly, this alternation is based on a subjective evaluation of cue reliability. In summary, this thesis will present relevant and new findings for better understanding spatial strategy formation, learning and representing spatial relations in memory, and multimodal cue combination.

An important and overarching aspect of this thesis is the characterization of individual differences in the context of human spatial navigation. Specifically, my research revealed individual differences in three areas: First, in utilizing egocentric or allocentric reference frames for spatial updating, second in individualized qualitative changes of space perception during long-term sensory augmentation, and third, in preferences to use native or augmented information in a cue combination task. Most importantly, I will provide a better definition and understanding of these individual differences, by combining qualitative and quantitative measures and using latest technologies such as online data recordings and interactive experimental setups. In fact, in the real world, humans are very active beings who follow individualized spatial cognitive strategies. Studying such interactive and individualized behavior will ultimately lead to more coherent and meaningful insights within the human sciences.

Table of Content

1. Synopsis

During the last four years, I investigated different aspects of human navigation and sensory processing. In total, my colleagues and I conducted five different studies and consequently we drafted five manuscripts out of this research, which will be the main content in this dissertation. In order to enhance the readability and the structure of this thesis, I will refer to these studies with a number (1 to 5) and their respective project names. Three of the manuscripts are already published, one manuscript is accepted and currently in press, and the last one is submitted. In order to integrate these different studies and results, I decided to write a synopsis. As described in the abstract, the experiments and results that I want to present in this dissertation can be categorized into three main subtopics of human spatial cognition. Hence, in each of the following three sections I will provide a literature review about the subtopic and give a detailed description of my own studies, including the respective results. An integrative discussion about all my studies will be provided in the last section of this chapter. However, it is important to point out that even more detailed descriptions of the experimental setups and the results for each study can be found in the respective manuscripts (chapter 2-6). The last chapter (chapter 7) will then focus on the implications of my research and on the outlook for future investigations.

1.1 Reference Frames in Human Navigation

This first section is centered on the topic of reference frames. Introducing this concept, I will start with stating how reference frames are related to sensory processing (Burgess, 2008) and then gradually explain their relation to human navigation (Klatzky, 1998). Next, I will elaborate about the neural underpinnings of egocentric and allocentric navigation and towards the end of this section explain how people use reference frames for building up individual spatial strategies (Gramann, Müller, Eick, & Schönebeck, 2005; Gramann, Müller, Schönebeck, & Debus, 2006). The main research question of this section will then be: Which navigation strategies do humans use and how do the proclivities for a certain strategy develop? The results of my first online navigation study will then provide an answer about which strategies exist and how stable these preferences are (Goeke, König, & Gramann, 2013). Consequently, the follow-up online navigation study will provide a first idea about how these reference frame proclivities may have emerged (Goeke et al., 2015).

Reference Frames in Sensory-Motor Processing

We as humans sample different kind of information from the environment via specialized sensory organs. The photoreceptors in our eyes are sensitive to light, hair cells in the cochlea are responsive to sound waves, other hair cells in the semicircular canals react to acceleration, and again different types of proprioceptors in our skin react to pressure and temperature. However, it is important to point out that the electrical signals, which are elicited by these different receptor types are initially coded in different reference frames (Burgess, 2008; Soechting & Flanders, 1992). One of the most prominent features of such a reference frame is given by its underlying coordinate system. This means that the activity of a neuron with an eye-centered reference frame is modulated by eye movements but not by head or body movements. In fact, there are many different reference frames. For instance, our sense of balance (the vestibular system) is activated through head movements and consequently, the neural responses of the semicircular channels are coded within a head-centered coordinate system. However, the activation of the photoreceptors on our retina is coded in eye-centered coordinates (Soechting & Flanders, 1992). Hence, it is crucial to generate a mapping between the two different underlying reference frames in order to combine vestibular and visual information for the purpose of navigation. This mapping can become even more complex when actions are involved. This is due to the fact that movements of different body parts are again coded in different reference frames; hand movements are coded in hand-centered coordinates, while leg movements are coded in leg-centered or body-centered coordinates (Cohen & Andersen, 2002). Furthermore, the representation and remapping of different reference frames follows a hierarchical order. A hand-centered reference frame can thereby be remapped into an arm-centered reference frame, which again can be transformed into a body-centered reference frame. However, such a remapping process is typically implicit and does not require deliberate attention. Figure 1 illustrates an example of such a coordinate transformation between eye-centered and body-centered reference frames for the purpose of grabbing an object. For a detailed discussion see Burgess (2008). In summary, processing of sensory information and generating appropriate actions requires a constant remapping of reference frames and their underlying coordinate systems.

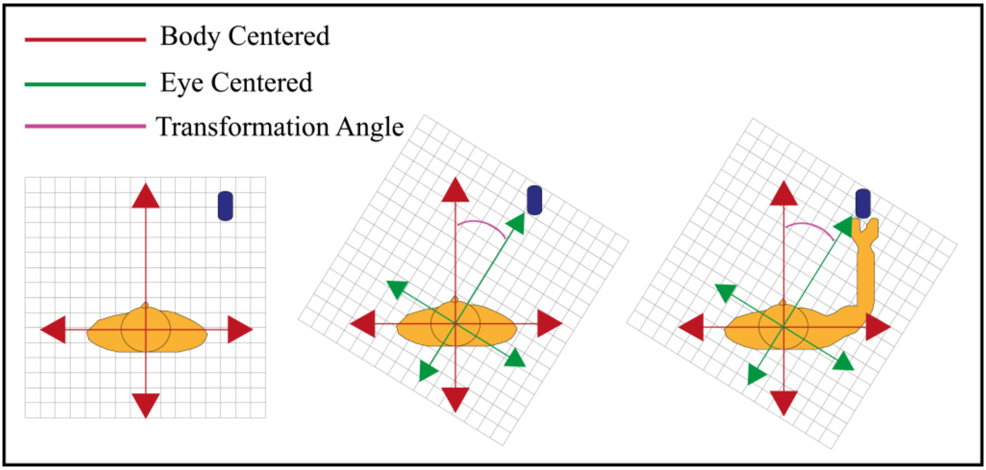

Figure 1: Remapping of reference frames. The body-centered (egocentric) reference frame (red) is centered within the agent and changes upon body movements. Fixating an object (blue) with our eyes creates an activation of the photoreceptors, which are coded in eye-centered coordinates (green). Based on the transformation angle (magenta), the visual information has to be re-transformed into body-centered (finally into arm and hand-centered) coordinates, in order to generate the appropriate action, here grabbing the object.

Although important in sensory processing, reference frames are not only required to map and combine different types of sensory input, but humans use them to represent themselves and other entities in space (Colby, 1998). Regarding human spatial cognitive processing, two major reference frames have been identified, the egocentric reference frame and the allocentric reference frame. The egocentric reference frame is defined by being centered within the agent and being dependent on the current physical position and orientation of that person. Opposite to that, the allocentric reference frame is defined as being independent of the orientation or position of the agent (Klatzky, 1998). A good example for using an egocentric reference frame in spatial navigation is to follow instructions like: “Turn right at the church and you will find our store 200 meters further down the road on the left-hand side”. In other words, references as “left” or “right” are inherently egocentric. A good example for using an allocentric reference frame is navigation based on GPS coordinates. No matter where the navigator is located on such a map, the representation of objects based on their GPS coordinates remains the same. Although there are clear differences between both types of spatial reference frames, in many circumstances, humans are capable of using either reference frame for navigation. In this respect, Redish and Touretzky proposed that human navigation is based on four different spatial representations; two of these representations are based on an egocentric reference frame, the other two on an allocentric reference frame (Redish & Touretzky, 1997). However, more recently, some researchers developed integrated theories and suggested that egocentric and allocentric representations exist in parallel and combine to support behavior according to the task (Burgess, 2006; Gramann, 2013). Figure 2 graphically illustrates the difference between egocentric and allocentric reference frames.

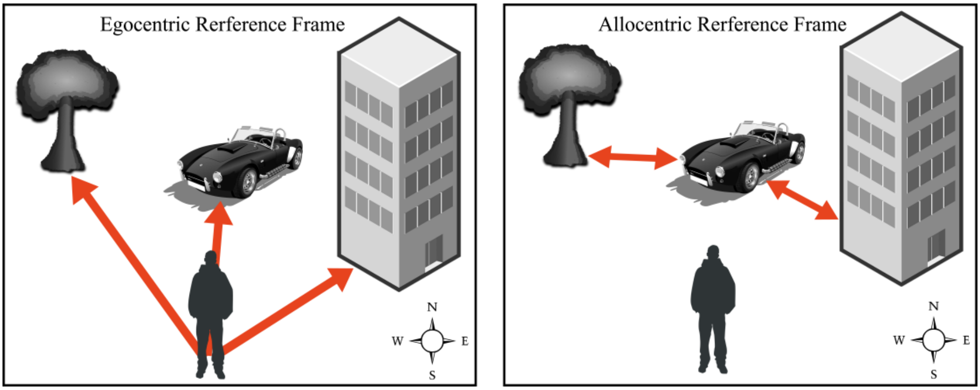

Figure 2: Egocentric (left) and allocentric (right) reference frames. The reference frames are depicted in red. An egocentric reference frame originates within the navigator and changes according to her/his orientation and position in space. Hence, in the left panel, the car is in front of the person, while the building is in front and right of the person. An allocentric reference frame is independent of the navigator; hence, the tree is west of the car, while the car is northwest of the building.

Gender and Age Differences in Human Navigation

Studying human navigation requires understanding about why different groups of individuals show different levels of performance as well as why different strategies (i.e. reference frames) are used in solving spatial tasks. Two of the most prominent spatial cognitive tasks are the so-called Morris water maze (Morris, 1984), and the mental rotation task based on the design of Shepard & Metzler (1971). Both tasks are graphically presented in Figure 3. The Morris water maze was originally developed as a setup for studying rodent behavior (Gallagher, Burwell, & Burchinal, 1993; Lindner, 1997; Perrot-Sinal, Kostenuik, Ossenkopp, & Kavaliers, 1996). However, more recently several studies have created virtual versions of the test to investigate human navigation. In a typical setup, the test subject has to find a platform, which is hidden under water and therefore cannot be seen (in the learning phase the platform was visible). Landmarks and other cues can help to orient and remember the location of the platform. Using such a setup, many studies reported that men outperform women in this task (Astur, Ortiz, & Sutherland, 1998; Newhouse, Newhouse, & Astur, 2007; Woolley et al., 2010). Furthermore, Driscoll and colleagues, as well as Newman and colleagues, reported that performance in the Morris water maze declines with age (Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005; Newman, Kaszniak, Newman, & Kaszniak, 2007). In a typical mental rotation study, the task requires that the subject recognizes visually presented objects from different viewing angles. In order to do so, the subject has to mentally rotate the objects in space. Are the gender differences reported in the Morris water maze also present in the mental rotation task? To answer this question, Masters and Sanders performed a meta-analysis reviewing data from 14 former studies (Masters & Sanders, 1993). In fact, they reported that males performed better than females in every single study, and furthermore showed that the effect size remained identical throughout the studies. Other studies also investigated the role of age in mental rotation and most of them reported a reduced reaction time and increased error rates in elderly subjects (Berg, Hertzog, & Hunt, 1982; Cerella, Poon, & Fozard, 1981; Collins & Kimura, 1997; Geiser, Lehmann, & Eid, 2008; Hertzog, Hertzog, Rypma, & Rypma, 1991).

Besides differences in performance, several researchers investigated differences in the use of spatial strategies, regarding the factors age and gender. In this respect, Lawton reported that women used a different wayfinding strategy than men (Lawton, 1996). In congruence, Dabbs and colleagues reported that when giving directions, women rely more often on landmarks and egocentric descriptions (left, right), while men use more abstract concepts and allocentric wording (north, south) (Dabbs, Chang, Strong, & Milun, 1998). Adding more evidence, Sandstorm and colleagues showed that females use landmarks more often than males (Sandstrom, Kaufman, & Huettel, 1998). Other studies combined performance and strategy measures to show that females perform better using egocentric compared to allocentric spatial strategies (Astur et al., 1998; Rizk-Jackson et al., 2006; Sandstrom et al., 1998; Saucier et al., 2002). Several studies also reported a decrease in the use of allocentric navigation strategies in elderly subjects (Holdstock et al., 2000; Iaria, Palermo, Committeri, & Barton, 2009). In summary, one can conclude that the degree and characteristics of gender and age-based differences are still discussed. However, most researchers agree that both factors influence navigation performance as well as the preference to use a particular navigation strategy.

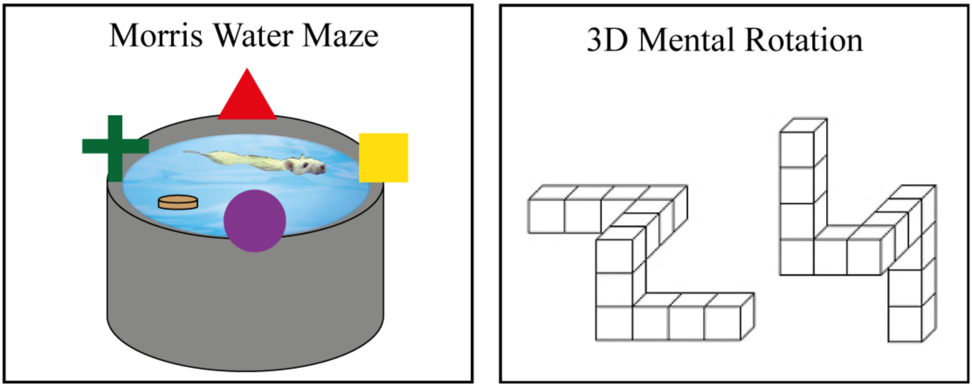

Figure 3: Morris water maze (left) and 3D mental rotation task (right). In the Morris water maze a platform is hidden underwater (only visible during training). The rodent has to use the spatial cues on the edge of the water tank to find (remember) the most efficient way onto the platform. In the mental rotation task, the subject has to spatially align the two shapes in order to judge whether they are identical (same shape from a different perspective) or not.

Neural Basis of Spatial Navigation

What are the neural underpinnings of egocentric and allocentric based navigation? One of the most outstanding findings in this respect was made by O'Keefe & Dostrovsky more than 40 years ago. The researchers were recording activity of neurons in the dorsal part of the hippocampus while rodents were freely moving in the environment. Unexpectedly, they found that neurons in this area always fired when the rat was at a certain place in the environment. Consequently, they called these neurons "place cells" (O'Keefe & Dostrovsky, 1971). Based on that finding, the hippocampus in general and place cells in particular became associated with spatial memory and map like mental representations (Broadbent, Squire, & Clark, 2004; Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999; Olton & Papas, 1979). In fact, the place cell network can be understood as the neural representation of allocentric navigation (O'Keefe, 1991). More recently, Moser and colleagues were investigating the question: "What kind of information could serve as an input to the hippocampal place cells?" Also recording neural activity in rodents, they found cells in the entorhinal cortex, which fired whenever the animal had traveled a certain distance in one direction. Overlaying the firing pattern of such a neuron with a spatial map of the environment showed the effect very clearly. The response properties of these neurons can be nicely described as a grid, respectively these cells were called "grid cells" (Hafting, Fyhn, Molden, Moser, & Moser, 2005; Moser, Kropff, & Moser, 2008). Based on their response properties grid cells are thought to be the basis for navigation based on egocentric reference frames, for instance in path integration. Findings of both place cells and grid cells also have been reported in humans (Ekstrom et al., 2003; Jacobs et al., 2013). Furthermore, several studies provided evidence that grid cells are functionally coupled to place cells (Solstad, Moser, & Einevoll, 2006). Further evidence for the function of place and grid cells came from navigation studies employing the Morris water maze paradigm. In particular, these studies showed that selective lesions in the entorhinal cortex and hippocampal regions impaired navigation performance in rodents (Logue, Paylor, & Wehner, 1997; Nagahara, Otto, & Gallagher, 1995). Figure 4 demonstrates the prototypical firing patterns of both place and grid cells overlaid with a map of the environment. As shown, the activity of the place cell is highly localized at a certain object (e.g. a particular house), while the grid cell fires whenever a certain distance is traveled in one direction, independent of the objects in space. Overall, the findings of place cells and grid cells provide a clear neural basis for allocentric and egocentric navigation.

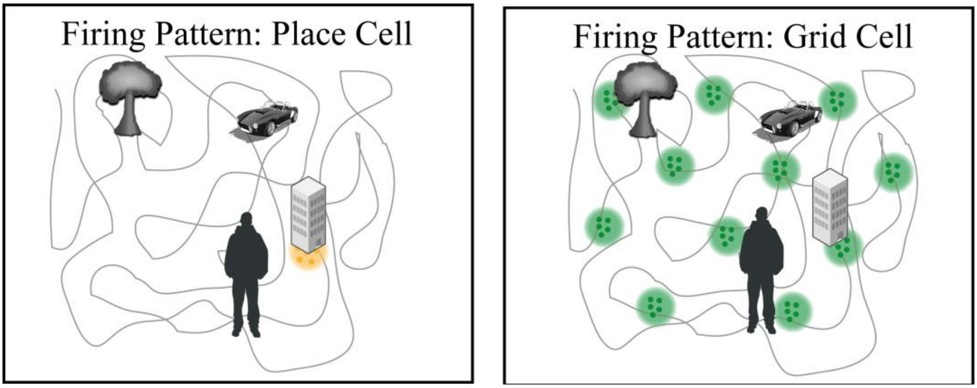

Figure 4: Firing patterns of a place cell (left) and a grid cell (right). The

orange dot indicates the firing pattern of the place cell; the green dots indicate the firing pattern of a grid cell. As shown, a place cell only fires when the subject is close to a particular object in space. A grid cell fires whenever the subject has travelled a certain distance into one direction.

Although the discoveries of place cells and grid cells are of enormous importance for the field of spatial navigation, we should ask the question: “Can the navigational networks subserving the computation of egocentric and allocentric reference frames be identified while humans actively solve a navigation task?” Within the last decade, several studies attempted to answer this question using functional Magnetic Resonance Imaging (fMRI). Maguire and colleagues showed that activity in the right hippocampus is associated with knowing accurately where places were located, while moving between these familiar places activated the right caudate nucleus (Maguire, Burgess, Donnett, Frackowiak, Frith, & O’Keefe, 1998). In another study, Maguire and colleagues demonstrated that grey matter volume in the posterior hippocampus was associated with taxi-driving experience, suggesting that plasticity in this brain region reflects the survey or map-like knowledge, which taxi drivers acquire with years of experience (Maguire et al., 2000; Maguire, Woollett, & Spiers, 2006). Iaria and colleagues differentiated between spatial learning and retrieval and reported that the anterior hippocampus is involved in the formation of a cognitive map, while the posterior hippocampus is used to retrieve spatial information (Iaria, Chen, Guariglia, Ptito, & Petrides, 2007). Vallar and colleagues implemented a task, which required egocentric processing and identified a network of posterior-parietal and lateral-frontal premotor regions as the underlying neural correlate (Vallar et al., 1999). Similarly, Galetti and colleagues performed a color judgement task and showed that a right-hemisphere fronto-parietal network is involved in the processing of egocentric information (Galati et al., 2000). In fact, many researchers agree that the parietal lobe is involved in the processing and updating of egocentric spatial information (Colby & Goldberg, 1999; Stein, 1992). Overall, the human navigational network has been identified on a structural basis by employing fMRI measurements.

Other researchers used again a different methodological approach and studied neural oscillations during navigation. Kahana and colleagues conducted subdural recordings in epileptic patients and found that the strength of theta oscillations is associated with complexity (Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999) in a navigation task. Gramann and colleagues promoted the so-called “tunnel paradigm”, an experimental setup in which participants can either use an egocentric or an allocentric navigation strategy (Gramann et al., 2005). In a study from 2010, the researchers reported a differential pattern of activation depending on whether subjects employed an egocentric or an allocentric strategy. Subjects using an egocentric perspective had a stronger amount of alpha desynchronization in primary visual cortex. In contrast, subjects following an allocentric strategy exhibited stronger alpha blocking in occipito-temporal, bilateral inferior parietal, and retrosplenial cortical areas (Gramann et al., 2010; Plank, Müller, Onton, Makeig, & Gramann, 2010). Using a similar paradigm, Chui and colleagues reported that parietal alpha desynchronization during encoding of spatial information was correlated with navigation performance when subjects used an egocentric reference frame, while retrosplenial and occipital alpha desynchronization was correlated with performance for subjects using an allocentric reference frame (Chiu et al., 2012). Overall, neural correlates of egocentric and allocentric navigation have been identified on different levels in the neural hierarchy.

Individual Differences in Reference Frame Proclivities

The aforementioned "tunnel paradigm" has been used in the last decade in several experimental setups and has demonstrated to reliably separate egocentric and allocentric navigation strategies (Gramann et al., 2005, 2006, Riecke, 2008, 2012). Having the possibility to freely choose and determine the reference frame proclivity in a navigation task, opens up new possibilities. In particular, one can ask the question: "Do humans exhibit stable preferences for navigation based on one reference frame or do people switch rather arbitrarily between egocentric and allocentric-based navigation?" My first online navigation study (study one) was centered around this question (Goeke, König, & Gramann, 2013). For this purpose, I programmed a website and employed an online version of the "tunnel paradigm". With such an online data acquisition approach, we could reach many more subjects than traditional lab-based recordings. Consequently, in this first study, we used data from 300 subjects. Each subject had to perform a virtual pointing task in 24 trials, in which the participant could use either an egocentric or an allocentric strategy. Additionally, two catch options were included to detect people without task awareness (erroneous responses). After this task was done, a short questionnaire was filled out by each subject. The main analysis then investigated whether the preference to use one particular reference frame was constant throughout trials or not. Most importantly, our results demonstrated that about 90%

of the subjects possess stable and strong preferences for using a particular navigation strategy. About 34% of the subjects consistently used the egocentric reference frame (Turner) and about 46% of the tested population consistently used the allocentric reference frame (Nonturner). Besides these two stable strategy classes, we found a third pattern of responses. About 8-10% of the subjects consistently switched reference frames from an egocentric reference frame in yaw rotations to an allocentric reference frame in pitch rotations. Arguably, this strategy is most similar to terrestrial navigation, where changes in the horizontal plane (yaw) are many times accompanied by head movements and changes in elevation (pitch) are typically not. Gramann and colleagues also observed such behavior in a study from 2012 (Gramann, Wing, Jung, Viirre, & Riecke, 2012) and concluded that it might arise due to the reduced ecological validity and a stronger visual-vestibular conflict in pitch rotations. However, our study first showed that such a switcher strategy is only present in one direction (yaw-ego, pitch-allo). The remaining subjects (about 10%) did not follow a clear (predictable) strategy, but rather switched randomly between egocentric and allocentric reference frames. However, a further observation, which supports the idea of stable reference frame proclivities for the majority of subjects, is the fact that people exhibited prolonged reaction times in those trials where they use a reference frame different to the individual preferred one. For instance, if a person preferred the egocentric reference frame (by using it more than 80% of the time), but in a few trials chose the allocentric reference frame, we observed longer reaction times in these trials. The reversed pattern was found for subjects who preferred the allocentric reference frame. This indicates that a switch in reference frame use requires some sort of remapping or attention shift that takes time. In summary, our study showed which stable strategy classes exist and it provided the first estimate how these strategies are distributed within the overall population.

When reference frame proclivities are so stable, what influences individual subjects to develop such preferences? Are these preferences driven by genetic, “nature-based” factors such as gender and age, or do other environmental, “nurture-based” factors play a vital role here? Gramann (2013) argued that individual reference frame proclivities might be influenced by socio-economic factors. Hoffmann and colleagues even argued that sex differences in spatial performance partly disappear when nurture is taken into account (Hoffman, Gneezy, & List, 2011). In order to shed light on this issue, we performed a follow-up study of the tunnel paradigm, again using the online version of the task (Goeke et al., 2015). In this follow-up project (study two), we established cooperation with about a dozen institutes worldwide and translated the web page into 10 different languages. By this approach, we recorded and consequently analyzed data of more than 1800 participants from over 25 counties. The focus of this investigation was to determine which factors influence navigation performance (reaction time and error rate) and, most importantly, navigation strategy based on reference frame proclivity. In congruence with the majority of former studies, we found that navigation performance was modulated by the factors gender and age (Astur et al., 1998; Gallagher et al., 1993; Masters & Sanders, 1993; Moffat, 2009; Moffat, Hampson, & Hatzipantelis, 1998; Newhouse et al., 2007; Rodgers, Sindone, & Moffat, 2012). As expected, young males outperformed elderly females. However, new insights were revealed by the analysis of reference frame proclivity. In particular, our results demonstrated that Latin Americans strongly preferred the egocentric (Turner) strategy, while North Americans preferred the allocentric perspective (Nonturner). Asians and Europeans were in between these extremes. Brown and Levinson showed that languages of indigenous tribes lack egocentric descriptions but instead contain more allocentric terms (Brown & Levinson, 1993; Levinson, 1997). However, nowadays most Latin Americans speak either Portuguese or Spanish, both languages that do have egocentric and allocentric words. Hence, it seems unlikely that language use was the driving factor of the observed differences in our study. Other cultural studies concentrated on the comparison between Eastern (collectivistic) and Western (individualistic) cultures (Chua, Boland, & Nisbett, 2005; Markus & Kitayama, 1991; Masuda & Nisbett, 2001). However, the observed differences in our study did not vary between Eastern and Western cultures. In summary, we could show that the preference for using a certain reference frame was strongly influenced by the cultural background, but neither by the gender or the age of participants. These results emphasize the need to take nurture-based factors such as socio–economic variables into account when studying human navigation.

1.2 Spatial Navigation & Theories of Cognition

The former chapter described and differentiated between navigation strategies based on egocentric and allocentric reference frames. However, besides the adoption of a certain navigation strategy, based on a set of reference frames, many other factors are important for real world spatial navigation. In particular, active navigation requires that we retrieve existing knowledge about the environment and simultaneously update our knowledge (learn) based on the new incoming information. Hence, in the following section I will proceed with elaborating about higher cognitive functions of navigation, including learning and representing spatial relations in memory. Here, a special focus is put on theories of cognition (Chomsky, 2006), comparing the classical representationist view (Marr, 1982) to more recent embodied theories of cognition (O'Regan & Noe, 2001; Thompson & Varela, 2001). After explaining these theoretical foundations, I will raise the question of how to test for an embodied theory of cognition within the domain of human spatial navigation? To answer this question, I will first introduce the alignment study (study three), in which we empirically compared the representationist view with an embodied theory of cognition for representing spatial information (Goeke, König, Meilinger, & König, submitted). Then, aiming to deepen the understanding of spatially embodied processes, I will explain the concept of sensory augmentation. Consequently, towards the end of this section, I will report about the feelSpace (study four), in which we investigated the long-term training effects with such an augmentation device, (König et al., in press).

From Behaviorism to Cognitivism

Throughout history, various attempts have been made to develop a unified theory that explains the human mind, with a particular focus on perception and consciousness (Caston, 2002; Faugloire & Lejeune, 2014; Kant & Guyer, 1998; Wittgenstein, 1980). In the early 20th century Behaviorism was the dominant theory in psychology (Skinner, 2011; Watson, 1913). However, the theory of Behaviorism neglected the absence of mental states and cognition, which both play a vital part in human behavior (Chomsky, 2006; Neisser, 2014). Hence, during the second half of the 20th century, most psychologists abandoned Behaviorism and instead turned to a cognitive theory of the mind. This cognitive theory of the mind (Cognitivism) supposes that we cannot perceive the world as it actually is. Instead, it states that we construct a representation of the world, using the (possibly flawed) input that we get from our senses. According to this theory, learning, decision making, and all other cognitive operations are based on such internal representations. In 1982, Marr developed a computational model of vision based on such a representationist perspective (Marr, 1982). Most importantly, Marr argued that in order to understand a complex process such as vision, we must separate three levels of abstraction, which are built on top of each other. At the top level of this hierarchy is the computational theory or abstract goal. At the intermediate level is the definition of the algorithm, which transforms the input into the desired output, and at the third and lowest level is a description of the 'hardware' and how it is physically engineered. The idea that the mind consists of such a layered architecture of representations has received great approval throughout many decades (Oliver, Garg, & Horvitz, 2004; Recce & Harris, 1996; Seibert & Waxman, 1989; Wang & Adelson, 1993). In fact, it seems that cognitivism based on a representationist framework captures many aspects of the human mind.

However, the idea of a detailed, image-like representation of visual information has also received critique from several researchers. Rensink and colleagues presented images to participants with a short blank period in between. The images strongly differed between each other (some objects were missing or had different colors etc.), however, participants failed to report these big changes. Consequently, this phenomenon was named "change blindness" (Rensink, Regan, & Clark, 1997). Figure 5 illustrates one example of such an experimental stimulus pair. Importantly, in a real experimental setup, both images would be shown repeatedly after each other. Big differences (e.g. the missing branch at the top of the right stimuli) would not be perceived by many subjects or only after a long presentation. Simmons and colleagues repeated the idea of the study, but this time the researchers developed a real world scenario and changed the person a participant was speaking to in a short interrupting moment (Simons & Levin, 1998). Surprisingly, about 50% of the participants did not notice that they spoke to a different person afterward. In congruence with these studies, Pessoa and colleagues investigated the blind spot and concluded that the result is not compatible with the representationist view (detailed image-like representation) of visual consciousness (Pessoa, Thompson, & Noë, 1998). In summary, the representationist approach is efficient in explaining several neural and cognitive processes. However, there are also clear shortcomings and counterexamples in which a pure representationist theory fails.

Figure 5: Example of stimulus pair in a change blindness study. Typically the two images are repeatedly shown after each other. However, even bigger changes (e.g. the missing branch at the top of the right stimulus) are not perceived by many of the subjects.

Embodiment & Sensorimotor Contingencies

Aiming to resolve the inconsistencies of a pure representationist view of cognition, the theory of embodied cognition emerged in the last decade of the 20th century (Varela, Thompson, & Rosch, 1991). Several different embodied theories of cognition have been suggested. However, all of them share the idea that the brain does not mainly create representations of the outside world, but instead all these theories stress the importance of the interconnection between the body, the brain, and the environment (Thompson & Varela, 2001; Thompson, 2007; Varela et al., 1991; Wilson, 2002). In particular, Varela, Thompson & Rosch (2001) criticized cognitivism because it doesn't account for the crucial feedback from action to perception. O'Regan and Noe developed the concept further and introduced a sensorimotor account of vision and visual consciousness (O'Regan & Noe, 2001). The authors called these sensorimotor associations "sensorimotor contingencies" or SMCs. Although O'Regan and Noe agreed that there are internal representations of visual information, they pointed out that these representations do not generate the experience of seeing. A good example for their idea is given by the following description of color perception.

"...suppose you are looking directly at the red patch. Because of absorption by the macular pigment, the stimulation received by the color-sensitive retinal cones will

have less energy in the short wavelengths when you look directly at the red patch, and more when you look away from the patch. Furthermore, since there is a difference in the distribution and the density of the different color-sensitive cones in central versus peripheral vision, with cone density dropping off considerably in the periphery, there will be a characteristic change in the relative stimulation coming from rods and cones that arises when your eyes move off the red patch. What determines the perceived color of the patch is the set of such changes that occur as you move your eyes over it."
(O'Regan & Noe, 2001)

Besides providing a solution for phenomena such as change blindness and the blind spot, this quote shows that the theory of SMCs provides an interesting idea of how qualitative experiences and visual consciousness could arise. In fact, O'Regan & Noe argued that complex feelings like "driving a sports car" cannot be described by bodily sensations. According to the authors, such feelings consist of the awareness of the sensorimotor contingencies, which are used and mastered in the current situation. For instance, the knowledge about how a car will respond to manipulations of its instruments.

A verifiable prediction of this theory is that action (in many cases) precedes and determines perception. In this respect, Kietzmann and colleagues investigated the perception of ambiguous figures and showed that the pattern of former eye movements determined which of two possible percepts was perceived (Kietzmann, Geuter, & König, 2011). Hence, the researchers concluded that action, in this case, precedes, and guides perception. Maye and Engel suggested the existence of object-related SMCs, which act on longer time scales (Maye & Engel, 2012). Furthermore, based on this assumption, they developed a computational model of SMCs and implemented this framework on a robot that explored the environment (Hoffmann, Schmidt, Pfeifer, Engel, & Maye, 2012; Maye & Engel, 2011). The final goal of such an approach is to develop artificial agents that act more naturally and behave more human-like in object recognition and object manipulation. Consequently, in a current review, Engel and colleagues argued that many findings of former studies can be re-interpreted in an action-oriented framework of embodied cognition (Engel, Maye, Kurthen, & König, 2013). Overall, we can say that the embodied approach provides a modern framework to study human cognition.

Embodiment & Spatial Cognition

How are the topics of embodied cognition and sensorimotor contingencies related to navigation? As a matter of fact, navigation is about (inter)active behavior with and within the environment. Hence, navigation is a good choice for empirical investigations, testing an embodied approach to human cognition. One of the first attempts in this regard was carried out by Zetzsche and colleagues (Zetzsche, Galbraith, Wolter, & Schill, 2007; Zetzsche, Wolter, Galbraith, & Schill, 2009). The researchers studied human navigation and manipulated the virtual environment such that there were severe violations of the Euclidean metric and planar topology. Interestingly, the performance in this condition did not differ compared to the situation when the environment was consistent with the geometrical properties of real physical space. As a consequence, Zetzsche and colleagues argued that humans do not use map-like representations, but rather SMCs for navigation. With regard to spatial navigation strategies, Meillinger and colleagues suggested that spatial SMCs might be important in complex situations when egocentric and allocentric reference frames combine (Meilinger & Vosgerau, 2010). In conclusion one can say that a few studies have tested and discussed sensorimotor theories in human navigation; yet, convincing empirical evidence supporting the theory of embodied spatial cognition has been sparse. Specifically, it is still an open question, which experimental paradigm is best suited for testing theories of embodied cognition in the domain of human navigation?

We addressed this issue by developing contrasting theories about how spatial relations between objects could be learned and stored in memory. The first theory states that we learn the absolute location and orientation of single objects, even though such information is not directly usable to navigate between objects. According to this theory, the information of two or more single objects is then cognitively combined in order to generate appropriate action plans (i.e. how to get from object A to object B). This theory is very efficient in terms of memory storage but less effective to generate fast and direct actions. Hence, this theory can be seen as the classical representationist view for spatial cognition. As an alternative, we proposed a theory that emphasizes the importance of actions in accordance with an enactive view of the human mind. In particular, this theory states that we do not learn unrelated information about an object's location and orientation. Instead, this model proposes that we directly learn how two (or more) objects are related to each other (i.e. how to get from object A to object B), while we navigate in the environment. Such a representation would be memory-wise rather unfavorable.

However, this kind of coding would have clear benefits for acting fast and directly, not requiring complex cognitive processes (i.e. aligning different coordinate systems and perspectives) before each action. To test and compare these two hypotheses, we developed two main tasks, which were tested in the so called "alignment study" (study three). In the first task the subjects were asked about the absolute cardinal orientation of single objects, and in the second task the subjects were asked about the relative orientation of two objects towards each other. Additionally, we varied the stimulus type (houses = localized objects, vs. streets=non-localized objects) and the response mode (3 sec vs. infinite time) (Goeke et al., submitted). Our results show that under time pressure subjects perform better in reporting how localized objects (houses) are related to each other, compared to judgments of absolute cardinal direction for single objects. However, when we increased the response time window to allow for cognitive strategies, or tested non-localized objects (streets), absolute judgments were better than relative ones. Together this pattern of results suggests that humans learn and store object-to-object (binary) relations in memory. This again supports two conclusions: First, it suggests that spatial relations in memory do not merely create an efficient representation of the world, but instead are coded such that we can directly perform relevant actions. Second, non-egocentric reference frames, in the form of object-to-objects relations, are compatible with an enacted theory of human spatial cognition. Overall, we therefore conclude that an enacted theory of the mind is compatible with spatial cognitive operations.

Learning New Sensorimotor Contingencies

In the aforementioned alignment study (Goeke et al., submitted), we provided evidence for the idea that humans learn and store action plans during real world navigation. Such a behavior can well be formalized within the framework of SMCs. In this view, the brain learns to associate a certain motor action (i.e. walking from A to B) with the respective change of sensory input. However, the creation of such (new) sensory-motor contingencies is limited by the type of the sensory stimuli provided. In many situations, visual information is dominant (Felleman & Van Essen, 1991), and therefore also plays a vital role in the creation of SMCs. However, not all aspects of space can be detected with our eyes while walking through the environment. For instance, absolute cardinal directions (allocentric information) cannot be perceived directly. Hence, we either have to rely on complex environmental cues (e.g. the position of the sun) or we have to use a map to obtain such information. Interestingly, when we look at other species, we find that some fish and birds possess so-called "Ampullae of Lorenzini", by which they can detect magnetic fields, i.e., the magnetic field of the earth (Goldenweiser et al., 2012; Harada, Masaki Taniguchi, Hirofumi, 2001; Wiltschko, Traudt, Güntürkün, Prior, & Wiltschko, 2002). In other words, these species have a direct perception of an allocentric reference frame, which they can use to navigate over long distances. Going a step further, one can then raise the question whether it is possible to equip humans with such a sense? More specifically, can we create a device that enables people to sense allocentric information of space, and are humans capable of learning new sensorimotor contingencies based on such information? To answer this question, let us first look at a related topic, namely sensory substitution. In fact, sensory substitution devices already exist for many decades. These applications are particularly useful to substitute an impaired sense for patients (Bach-y-Rita, Collins, Saunders, White, & Scadden, 1969; Bach-y-Rita & Kercel, 2003). Bach-y-Rita and colleagues were among the first who build a so-called visual-to-tactile substitution device. This device recorded the visual scene with a camera and translated that image into an activation of tactile stimulators arranged on a 20 by 20 tactile array applied to the back of the participants. In other words, the patients were able to feel (very coarsely) what other people see (Bach-y-Rita et al., 1969). Over the last decades, several other sensory substitution devices have been invented that transform visual input to either acoustic or tactile stimulations (Auvray, Hanneton, & O'Regan, 2007; Deroy & Auvray, 2012; Maidenbaum, Levy-Tzedek, Chebat, & Amedi, 2013; Ptito, Moesgaard, Gjedde, & Kupers, 2005; Ella Striem-Amit, Guendelman, & Amedi, 2012). However, what if we do not want to substitute a sense, but rather augment (create a new) sensory perception, as mentioned in the earlier example regarding the allocentric information of space?

Addressing this issue, Nagel and colleagues build an early version of such an augmentation device, from now on called the "feelSpace" belt. In essence, the first version of this belt consisted of 13 vibro-motors and a compass and was worn like a belt around the waist (Nagel, Carl, Kringe, Märtin, & König, 2005). Figure 6 shows this first version of the feelSpace belt. Most importantly, only the vibro-motor which was closest to north was actively vibrating. Hence, when subjects wore it and moved around, a full body yaw rotation was accompanied by consecutive activation of all vibro-motors. In other words, the participants could "tactilely feel where north is" with respect to their own orientation. The study by

Nagel and colleagues focused on the training aspect with the augmentation device, so that subjects wore the belt continuously for 6 weeks and measurements were carried out before and after the training period. Overall, the results of this study indicated relevant changes in both navigation performance and the subjective feeling of space. However, the overall number of participants was rather low (N=4) and no physiological measurements were performed. Hence, appropriate statistical tests could not be carried out.

Figure 6: First version of the tactile sensory augmentation device, aka. feelSpace belt (Figure reprinted with permission of the senior author). The participants could wear the belt and were informed about the cardinal direction through tactile stimulation by one of the vibro motors.

Consequently, in a follow-up project also called the feelSpace study (study four), we aimed to overcome these shortcomings (König et al., in press). Hence, in a first step we developed a new and fMRI compatible version of the feelSpace belt. Furthermore, we choose a similar experimental design, in order to compare our follow-up study with the results of the former study. Thus, in our study, one group of participants trained 6-7 weeks with the belt, while a control group did train their navigation but without belt and also participated in the same measurements. The measurements itself were done before or in the beginning of the training as well as after the training period, in order to detect the training related changes. Most importantly, in our follow-up study we also included sleep EEG and fMRI measurements to test for physiological changes. As my contribution was centered on the sleep EEG analysis, I will focus here on these results. In particular, we found that subjects who trained with the augmentation device exhibited longer durations of rapid eye movement (REM) sleep in the first night of belt training compared to a baseline measurement. No such effect was found for the control group. In the time frequency analysis, we chose three different frequency bands (delta, theta, and sigma), which were representative for the three sleep stages (slow wave sleep, REM, stage 2). In fact, we found a significant decrease of sigma power in the first night compared to baseline. Again, this effect was only present in belt-wearing subjects but not in controls. Hence, the results show that training with the sensory augmentation device yielded changes in both sleep behavior (increased REM) and neural processes during sleep (decrease of sigma power in stage 2). Similarly, the fMRI results suggested that training with the augmentation device is associated with plasticity in sensory and higher motor areas. Furthermore, training with the feelSpace belt resulted in changes in the subjective perception of space and in confidence ratings for spatial tasks. However, in contrast to that, the behavioral tests revealed no performance improvement in a homing task after training. In summary, we can conclude that new sensorimotor contingencies, based on an augmented sense, can be learned. However, during an initial (six weeks) training phase changes are mostly of qualitative nature and are reflected by physiological properties, but are not (yet) measurable via improvements in navigation behavior.

1.3 Multimodal Processing & Sensory Augmentation

This third section of my synopsis will concentrate on multimodal processes. Hence, in the beginning of the chapter, I will explain the core concepts and observations in multimodal research. Thereby, the phenomenon of visual capture, (i.e. ventriloquist effect, Thurlow & Jack, 1973; McGurk effect, McGurk & Macdonald, 1976) will be explained from various perspectives. In a next step, I will then introduce the concept of Bayesian optimal integration (Ernst & Banks, 2002) and also discuss suggested requirements for such a process (Körding et al., 2007). As an alternative to Bayesian integration, I will then introduce the idea of Bayesian alternation, which recently has been observed in several studies. (Gori, Del Viva, Sandini, & Burr, 2008; Nardini, Jones, Bedford, & Braddick, 2008). Towards the end of this section, I will then combine the topic of multimodal processing with the idea of sensory augmentation, as described in the feelSpace study. The main research question for this chapter will then be: How do untrained humans combine information from a native and an augmented sensory modality? In the platform study (study five) we will address this issue and compare the Bayesian integration model with the Bayesian Alternation model for prediction of the bimodal performance (Goeke, Planera, Finger, & König, 2016).

Perceptions Are Multimodal

As reflected by the feelSpace study and other studies presented in this dissertation, successful navigation requires that we use visual, auditory, proprioceptive and other sensory information in combination. However, how all these different sensory information are combined in order to create a holistic perception of the world and to carry out reasonable actions is still widely discussed within the scientific community. Most researchers agree that sensory processing follows a certain hierarchy. Primary brain areas process simple features such as visually oriented gratings or acoustic frequencies, while areas further up the hierarchy process more and more complex features (Felleman & Van Essen, 1991; Kobatake & Tanaka, 1994; Ullman, Vidal-Naquet, & Sali, 2002). Hence, one of the most important questions in multimodal research is when and how the information from the different modalities is combined. Furthermore, it is important to find out how and under which conditions the percepts of one sense influence the percepts of another. As mentioned before, vision is the most dominant sense on both a perceptual and a neural level (Felleman & Van Essen, 1991). Still, sensory signals from several other senses are merged with our visual sensation to provide an even more robust and complete understanding of the environment. In fact, the presence of visual information can thereby have an impact on how we perceive other types of sensory information. This can create illusions in which we perceive the world different than it actually is. A good example for such an illusion is the famous ventriloquist effect (Thurlow & Jack, 1973). Ventriloquists are street artists who entertain the audience by moving a puppet and simultaneously speak without moving their lips. As the puppets mouth is moved according to the sound produced, the sensation arises that the sound actually originates from the puppet rather than from the mouth of the ventriloquist. However, the effect is more general than it seems at first. We all experience this phenomenon when we sit in front of a television and watch TV. The sound is emitted by the speakers, which are usually on the side of the monitor, while the actors move (their lips) on the center of the screen. Still, the sound is perceived to originate from the exact place where we see the mouth of the actors. This shows that the visual information is overruling the perception of auditory information. Over 30 years ago, McGurk & McDonald studied the influence of visual information on speech processing and found that the way we move our lips has a strong influence on what our conversation partner will perceive, even though the sound remains identical (McGurk & Macdonald, 1976). For instance, if a subject is exposed to the sound “gaga” but sees someone moving their lips as if the sound “baba” was pronounced, the subject will consequently not hear the (true) sound “gaga” but the sound “baba” instead. However, without seeing the lip movement the subject would hear “gaga” again. Ever since, this phenomenon is called the “McGurk effect”. Both the ventriloquist and the McGurk effect are examples of the phenomenon of visual capture, which states that visual information dominates and influences the perception of other senses.

Attention plays an important role at various stages of sensory processing. Hence, one could ask the question whether it is possible that visual capture can be understood as an attentional mechanism? In fact, Choe and colleagues argued that the ventriloquist effect was rather due to a shift in decision criteria than due to a perceptual change (Choe, Welch, Gilford, & Juola, 1975). However, more recently Bertelson and colleagues investigated the ventriloquist effect and showed that ventriloquism does not require deliberate visual attention (Bertelson & Driver, 2000). Similarly, Vroomen and colleagues concluded that ventriloquism does not depend on attention but instead reflects automatic sensory interactions (Vroomen, Bertelson, & de Gelder, 2001). Overall, a majority of researchers nowadays agrees that visual capture happens also in the absence of visual attention (Helbig & Ernst, 2008).

Multimodal Integration is based on Bayesian Principles

The topic of visual capture becomes particularly interesting when visual information is impaired, either naturally (e.g. in darkness) or artificially (e.g. by blurring the visual input). Ernst and Banks developed a clever setup, in which they could manipulate the accuracy of the visual system while subjects had to judge the size of objects using visual and/or haptic information. Consequently, each subject had to perform the task in three conditions, once given only visual information, once given only haptic information, and once given both visual and haptic information. Additionally, the noise parameter for the visual system was varied. Analyzing the subjects' behavioral responses, the authors were able to predict the bimodal performance ($\sigma^2_{combined}$) from the unimodal performances (σ^2_{visual} and σ^2_{haptic}), assuming that the participants' decisions were based on a Maximum Likelihood Estimation (MLE) model as shown in the equation 1. The basic functionality of this model is outlined in Figure 7.

$$(1) \qquad \sigma^2_{combined} = \frac{\sigma^2_{visual} \cdot \sigma^2_{haptic}}{\sigma^2_{visual} + \sigma^2_{haptic}}$$

In short, this model states that information from both senses (here visual and haptic) is used for the combined perception of the objects' size; however the relative contribution (weight) of each sense is determined by its normalized reciprocal variance (smaller variance leads to a higher weight). As the data showed, the relative weights of the haptic sense indeed increased with decreasing visual accuracy. Hence, the authors concluded that subjects behaved optimally according to the proposed MLE model (Ernst & Banks, 2002).

The paper by Ernst and Banks can be considered as a milestone in the area of multisensory processing. Accordingly, several follow-up studies confirmed that humans behave as predicted by the Bayesian integration model (Battaglia, Jacobs, & Aslin, 2003; Ernst & Bülthoff, 2004; Körding & Wolpert, 2004, 2006; Rosas, Wagemans, Ernst, & Wichmann, 2005). Usually, vision provides the most reliable information in the spatial domain, and as a consequence, it has the highest weight in the MLE model for spatial tasks. However, several studies have shown that the auditory system is more reliable in temporal judgments (Shams, Kamitani, & Shimojo, 2004; Shams, Kamitani, & Shimojo, 2000; Spence & Squire, 2003). Hence, in accordance with the MLE model, audition dominates vision in cases when temporal decision-making is required. Also the ventriloquist effect can be described according to the rules of Bayesian integration. Interestingly, Alais & Burr even showed that in situations where the visual information is strongly impaired, auditory dominance takes over such that the perception of the visual stimulus is biased by the location of the auditory source (Alais & Burr, 2004). In other words, the ventriloquist becomes reversed. Optimal integration also has been reported for visual and proprioceptive cues (Frissen, Campos, Souman, & Ernst, 2011; Reuschel, Drewing, Henriques, Rösler, & Fiehler, 2010) as well as for visual and vestibular signals (Butler, Smith, Campos, & Bülthoff, 2010). In conclusion, there is a vast amount of studies, which provide empirical evidence that humans integrate sensory information based on underlying Bayesian principles.

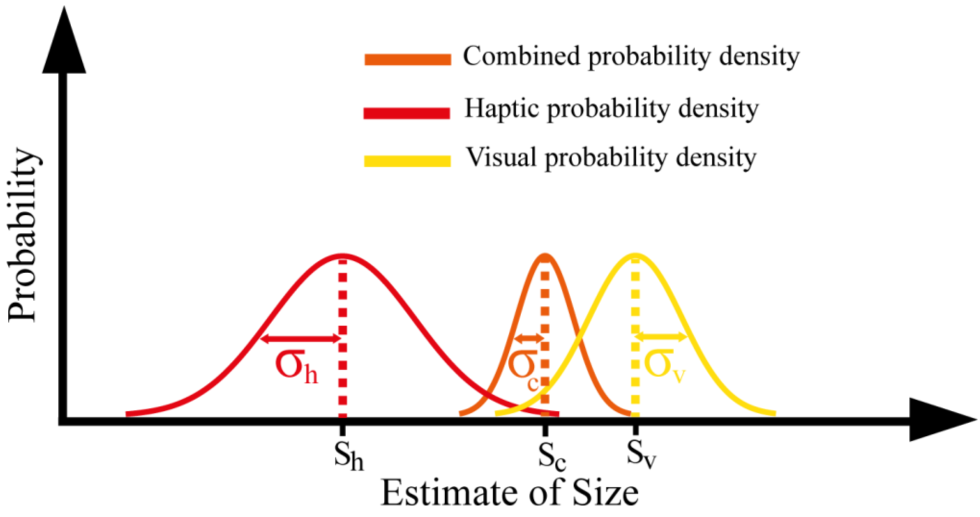

Figure 7: Example of multimodal integration based on the Maximum Likelihood Estimation (MLE) model. In this example, the task is to judge the size of an object (abscissa). Relevant information is received via visual and haptic sensors. All sensory estimates ($S_{h,v,c}$) are described by a Gaussian

probability (ordinate). The position on the abscissa shows the bias of the sensory input, while the variance (σ) of the Gaussian reflects the precision of the sensory information. Therefore, high variance indicates unprecise information. In the example, the haptic sensation (S_h) is more unprecise (higher σ) than the visual sensation (S_v). Hence, the combined percept (S_c) is more similar to the pure visual estimate. Importantly, the bimodal variance (σ_c) is smaller than both unimodal variances, reflecting the perceptual benefit of multisensory integration.

Prerequisites & Exceptions to Sensory Integration

As described, humans are capable of integrating different sources of sensory information. Thereby, multimodal sensitivity and performance is improved. Still, it is left to explain how we learn which signals to combine and which not? To emphasize the importance of this process, let us consider the following example: Imagine an outdoor scene on a busy street, many people walk back and forth talking to each other, cars run in several directions. There are dozens of independent visual and auditory sources simultaneously. Still, our brain combines just the right sounds with the correct visual appearances such that we can navigate rather effortlessly in such a complex environment. How can this be achieved? Körding and Tenebaum suggested that our brain constantly tries to infer the underlying cause of all perceptual events and that two perceptual events (e.g. moving lips and speech), which share a common cause (somebody speaking), should be integrated while perceptual events with different causes should not be integrated. Consequently, they developed a Bayesian model that reflected this idea (Körding & Tenenbaum, 2006). Figure 8 shows a graphical illustration of this so-called *"causal inference model"*. Körding and colleagues tested the model a year later using an auditory-visual localization task. To simulate the behavior in this particular task, the model used four parameters; the uncertainty of the visual and auditory cues, a bias term for perceiving objects centrally and the prior probability that both cues had a common cause. In fact, the model predicted the perceived locations of visual and auditory cues in the bimodal condition better than any former proposed model (Körding et al., 2007). Going a step further, Parise and colleagues presented participants with sequences of temporally correlated or uncorrelated visual-auditory stimuli pairs. The results clearly demonstrated that a temporal correlation of the two signals increased multisensory integration in the spatial domain, thereby showing that correlation can be used to infer a causal relationship between two signals (Parise, Spence, & Ernst, 2012). No correlation (temporal or spatial) implies that there is also no causal relationship. Hence, it is a prerequisite that two sensory signals originate (or seem to originate) from the same event, in order to be integrated as described in the MLE model. Importantly, this also shows that causal inference mechanisms are not only relevant for higher cognitive functions, but also for automatic signal processing.

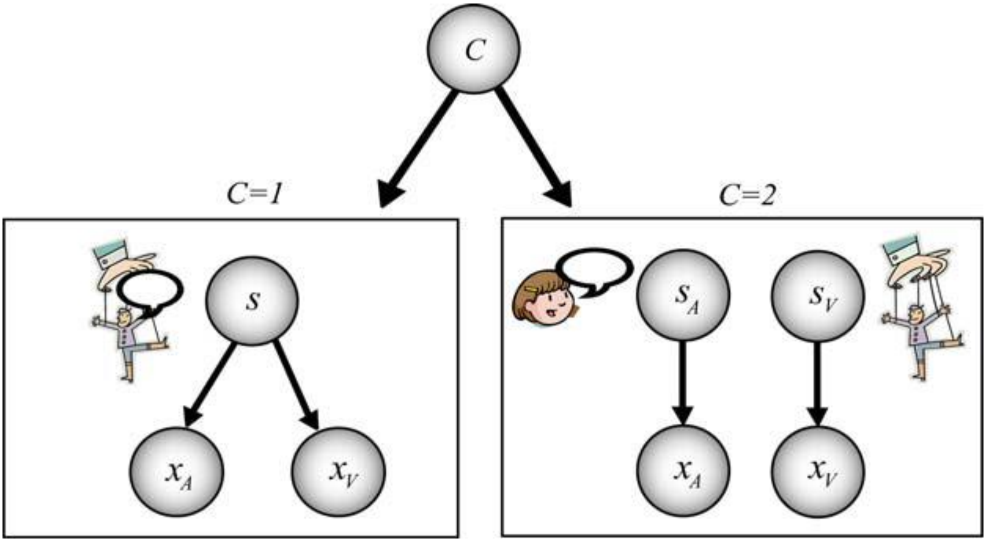

Figure 8: The causal inference model, as described by Körding & colleagues in 2007 (Figure reprinted with permission from the first author). The model compares two possible structures how the sensory information could have been generated. The left structure assumes that the two sensory cues (e.g. visual and auditory) have the same underlying cause; the right structure assumes two independent causes. The model then calculates the probability for both possible structures and then derives optimal predictions from this.

As shown before, the MLE model describes, for most situations, how two sensory signals are combined. However, there are also several cases in which researchers reported "sub-optimal" integration strategies. For instance, Liesker and colleagues found that the coordination of hand and eye movements is suboptimal in a search task (Liesker, Brenner, & Smeets, 2009). Consequently, some researchers suggested alternatives how two sensory cues could be combined. One of the main proposed alternatives is that people only use one cue at a time, but alternate (switch) in the usage between two cues based on their relative reliabilities. Serwe and colleagues compared the MLE model to such an alternation (cue switching) model in a visual-proprioceptive task and concluded that subjects indeed switched in cue use from trial to trial, without integrating between them (Serwe, Drewing, & Trommershäuser, 2009). More recently, De Winkel and colleagues provided further evidence that under certain experimental conditions humans rather alternate between two sensory cues, instead of integrating them into a combined percept (De Winkel et al., 2013; De Winkel, Katliar, & Bülthoff, 2015). In summary, cue combination strategies in humans can typically be described with an MLE based approach, however, there are some exceptions to that rule that need to be investigated more closely.

An interesting period regarding multisensory integration is childhood. Particularly intriguing is the question how MLE based cue combination is related to cognitive development and whether integration takes place right (or a few months) after birth, or whether this occurs much later? In 2008, Nardini and colleagues investigated precisely this question, and compared participants in three different age groups (children between four-five years of age, children between seven-eight years of age, and adults). The researchers employed a navigation task in which the subjects either used visual, proprioceptive, or both types of sensory information. In their analysis, they contrasted the prediction performance of the MLE model with a Bayesian cue alternation model and demonstrated that both groups of children switched between cue usage, whereas adults optimally combined both signals as described by the MLE model (Nardini et al., 2008). In the same year, Gori and colleagues investigated the ability of children to integrate vision and touch and reported that until eight to ten years of age, the cue combination strategy in children is far from optimal (Gori et al., 2008). Furthermore, Adams recently compared different cue combination models with an audio-visual temporal judgment task and provided further evidence that older participants employed a partial integration strategy while younger participants (<8 years) did not integrate, but instead switched between the two sensory signals provided (Adams, 2016). On the other side of the age spectrum, Bates & Wolbers investigated elderly individuals and demonstrated that cue combination becomes less optimal with age (Bates & Wolbers, 2014). Overall, there seems to be strong evidence that integration of sensory information requires a certain degree of behavioral development as well as the maturity and proper functioning of cortical structures.

Cue Combination & Sensory Augmentation

Applying the concept of sensory augmentation in the area of multisensory processing opens up further interesting questions. Arguably, sensory augmentation devices are most helpful when the native senses provide inaccurate or incomplete information such that the sensory augmentation device can help to speed up or improve decisions. In the domain of spatial navigation, a simple example of such a system is a driver assistance system. Newer versions of these systems emit auditory feedback when the driver drives backward. The frequency of auditory tone thereby codes for the distance of the car to any obstacle that is behind it. In other words, the auditory signal provides us with continuous information about spatial distance, which we can use for navigating the car. However, such a system is part of the car and does not feel as being part of our body. A few studies also addressed the topic of sensory augmentation in basic research. Quek and colleagues developed an apparatus that provided augmented haptic feedback in the form of skin stretch when subjects judged the stiffness of objects. As a result, the researchers reported that the augmentation device increased discrimination accuracy such that the subjects had a more fine-grained perception for the stiffness of objects when using the device (Quek, Schorr, Nisky, Okamura, & Provancher, 2013). Can these results be interpreted within the domain of multimodal processing? In fact, both the native (pressure) signal, and the augmented (skin stretch) signal were processed via proprioceptors. Hence, the mapping was not truly cross modal. A few years earlier, Ernst investigated whether people can (optimally) integrate two signals, which are usually not associated (Ernst, 2007). In the respective experimental setup, the stiffness of an object was artificially linked to the brightness of an object, while participants had to identify a distractor among 3 stimuli. After a one day training period, discrimination accuracy improved in the bimodal condition as predicted by the MLE model. This shows that humans are able to learn new associations of formerly uncorrelated sensory signals. However, both stiffness and brightness were processed with their respective native modalities (haptic and visual) such that there was no sensory augmentation. Hence, one question that remains is: How is sensory information combined when one source of information is mediated by an augmented modality and the other source of information comes from a native but different modality?

In the platform study (study five) we aimed to shed light on this issue (Goeke et al., 2016). For this purpose, we used a slightly different version of the tactile augmentation device that we already used in the feelSpace study.

Additionally, we build a platform to control angular rotation. In the experimental setup the rotation platform and the tactile belt were synchronized such that a rotation of the platform simultaneously activated the vibro-motors in a successive order. As a result, the subjects were informed about the angular rotations by both native (mostly vestibular) sensations as well as by the augmented tactile stimulation (in the bimodal condition). The task of the subjects was to indicate which of two consecutive angular rotations was longer in degrees. Importantly, all subjects were untrained, meaning that they never wore the tactile belt before. During the task, all subjects were blindfolded and wore noise canceling headphones so that the only available sensory cues were the (augmented) tactile vibration and the native (mostly vestibular) sensation. To test and contrast different models how native and augmented information could combine, all subjects performed the task in three conditions: In the first condition the task was performed using only the augmented tactile vibrations, without rotation of the platform. In the second condition the augmentation device was switched off such that there was only rotation information from the platform. In the third (bimodal) condition both the augmentation device and the platform rotation were switched on. After calculating individual just noticeable differences (JND's), we compared the different cue combination models (i.e. Bayesian Integration vs. Bayesian Alternation). Interestingly, the results demonstrated that the participants did not integrate the augmented and the native sensory information, as suggested by the MLE model. Instead, the study provided clear evidence that subjects switched between both cues, as described by the Bayesian Alternation Model. Moreover, calculation of cue weights based on subjective self-evaluations (questionnaire answers) yielded better prediction performance than the calculation of cue weights based on objective measures of cue reliability. In summary, we conclude that integration of sensory information is not established instantaneously in the case of sensory augmentation. Instead, our results suggest that a combined sensory percept requires experience and active training.

1.4 General Discussion

In this synopsis (section 1.1 - 1.3) I examined human navigation from three different aspects and illustrated my own contribution in the form of five studies. In summary, I started with two online studies that investigated navigation performance and individual proclivities to use a set of reference frames for navigation. The alignment study (study three) examined how spatial relations are stored in memory, while the feelSpace study (study four) investigated qualitative and physiological changes associated with long-term sensory augmentation. In the platform study (study five) I finally analyzed how such an augmented signal is combined with information from a native sensory modality. For each of these studies, I stated the most important results and conclusions. Even more detailed results and discussions will be provided in the respective manuscripts. Hence, in this section, I will pursue a different goal. In particular, here I will provide overarching topics, which have implications for most of my studies as well as for spatial cognitive processing in general.

Individual Differences in Processing Spatial Information

The first topic, which is addressed in most of my studies are individual differences in spatial cognitive processing. In the first online study we showed that humans have stable but distinct preferences in their navigation strategy (Goeke et al., 2013). An initial attempt to predict those strategy classes (i.e. the Turner from the Nonturner strategy) based on gaming and computer experience failed. However, in the follow-up study (Goeke et al., 2015), we could show that strategy use was strongly correlated with the participants' cultural background. An obvious remaining question is: What is meant with "cultural background"? In our study, we used geographical information (North America, Latin America, Europe, and Asia) to cluster the participants into four broad geographical classes. The idea behind this approach was that participants within these groups share many cultural properties. However, in future work it might be beneficial to collect further socio-economic variables, (e.g. first language, income, occupation, individualistic vs. collectivistic behavior, feeling of security etc.) in order to specify which exact factors determine reference frame proclivities. Interestingly, individual differences also played a major role in the platform study (Goeke et al., 2016), where we investigated how native and augmented sensory information are combined. On a group level, the Bayesian Alternation model yielded the best prediction results; however only when we employed subjective instead of objective weights for determining cue probabilities. Overall, individual differences in cue preferences were rather strong. Some subjects had a strong bias using only the native cue, some others exclusively used the augmented cue, and again many others alternated much more frequently between both. In fact, a few subjects (N=2 to 3) even showed a trend towards optimal integration between both cues. From these results, we can infer that the way how sensory information is combined, strongly differs between subjects and might be dependent on other, yet unknown, factors. Again, demographic and socio-economic parameters might help to better understand these differences. At last, the results of the feelSpace study (König et al., in press) were also characterized by individual differences. In particular, qualitative changes in space perception varied strongly between subjects. While some subjects understood the augmented signal mainly as a tactile compass, which points north, others projected the allocentric information onto objects in the environment (Kaspar, König, Schwandt, & König, 2014). Similarly, the performance of a few belt-wearing subjects clearly improved after training; however on a group level, these improvements were not robust and therefore not significantly different from the baseline measurement. Altogether, I conclude that the processing of spatial information is highly individualized. Throughout the different studies presented in this thesis, I showed that it is a promising approach to combine subjective and objective measurements in order to better understand and characterize these individual variations.

Spatial Relations & Reference Frames

The second major topic of this thesis is the use of spatial reference frames and the way we learn and memorize spatial relations. In the two online navigation studies (Goeke et al., 2015; Goeke et al., 2013) we showed that most people consistently use one out of three possible navigation strategies (Turner, Nonturner, and Switcher) to solve a virtual pointing task. These strategies are defined by the use of a certain reference frame and the axis of rotation. Although individual preferences are evidently strong, Gramann argued that egocentric and allocentric reference frames exist in parallel (Gramann, 2013). An interesting and still open question is whether the preference for a certain strategy has further consequences for other observations in spatial cognition? To my understanding, one promising approach is to look at the influence of gravitational information on the perception of subjective vertical information (Mittelstaedt, 1983). In that respect, Bury and Bock recently investigated in which way people adjust the vertical axis of a visual object when the whole body was rotated by 90°. Interestingly, the authors found that about half of the participants adjusted the object such that it was aligned vertically with their body axis (orthogonal to gravity), while the other half adjusted the object in accordance with the gravitational axis (orthogonal to their body axis) (Bury & Bock, 2016). These dichotomous responses are comparable to the Turner / Nonturner responses in our study and earlier versions of the tunnel paradigm (Goeke et al., 2015; Goeke et al., 2013; Gramann et al., 2005, 2012). In fact, in a joint effort with Bury and colleagues, we now aim to find out whether both phenomena are correlated. In any case, the three navigation strategies we observed should not be understood as a final list. Recently, Kiston and colleagues provided evidence for two possible further classes, namely, Nonmovers and Spinners (Kitson, Sproll, & Riecke, 2016). According to the authors: *"Nonmovers reacted as if they not only failed to update heading changes but also the movement itself, while Spinners responded as if they arrived at the end point, turned 180 to face the path, and then pointed to the origin from the new orientation"* (Kitson et al., 2016).

Furthermore, in the alignment study we provided evidence for the existence of non-egocentric (object-to-object) reference frames (Goeke et al., submitted). Similarly, other researchers extended the traditional division of egocentric and allocentric reference frames and introduced additional, object-based or intrinsic reference frames (Mou & McNamara, 2002; Schmidt & Lee, 2006). With respect to these findings, it might be interesting to combine the experimental paradigms of the alignment study and the feelSpace study. In the feelSpace study, we augmented subjects with the ability to "feel where north is". In other words, we projected a global, allocentric reference frame onto the waist of the subjects. However, the way how this signal was interpreted was remarkably different between subjects. While some subjects mostly talked about their "increased self-awareness of where north is" other subjects projected the allocentric information onto the environment. These subjects reported that they automatically compared and related localized objects (such as houses) with respect to their cardinal orientation. Therefore, wearing the feelSpace belt could lead to a facilitation of the object-to-object representations, as described in the alignment study. In summary, I conclude that the use of reference frames with the consequent formation of an individualized navigation strategy is one of the key mechanisms in human cognitive and perceptual processing. Knowing which strategies exist and how they emerge is crucial to reach a better understanding of human cognition.

SMCs & Interactive Experimental Setups

A third prevalent issue throughout this dissertation is the theory of sensorimotor contingencies (SMCs) as formulated by O'Regan & Noe (K. O'Regan & Noe, 2001). Figure 9 shows a graphical illustration of this theory and provides a short overview of how Bayesian cue combination and the influence of spatial strategies could be integrated within such an embodied framework. In the center of this illustration is the acting human being, who is navigating in the environment. During the movement, the sensory input (e.g. the visual input on the retina) changes. Furthermore, the efferent motor command (e.g. the leg movement) is propagated so that the change of the visual input can be combined with the respective motor output. This process of learning action-perception associations creates new SMCs or refines and improves existing ones (Mastering of SMCs). Such mastered SMCs are part of our procedural memory and thereby can also influence higher-level cognitive processes such as navigation strategies. However, existing SMCs are particularly useful as prior information in Bayesian cue combination, to infer properties such as cue reliability and the underlying cause of a cue (Körding et al., 2007). In this view, the mastery of SMCs leads to sensory integration and consequently to a combined percept. However, combining sensory information with untrained SMCs can lead to cue alternation (Adams, 2016; C. M. Goeke et al., 2016; Gori et al., 2008; Nardini et al., 2008). Based on the (combined) percepts, the task demands, and an individual strategy a new decision can be made.

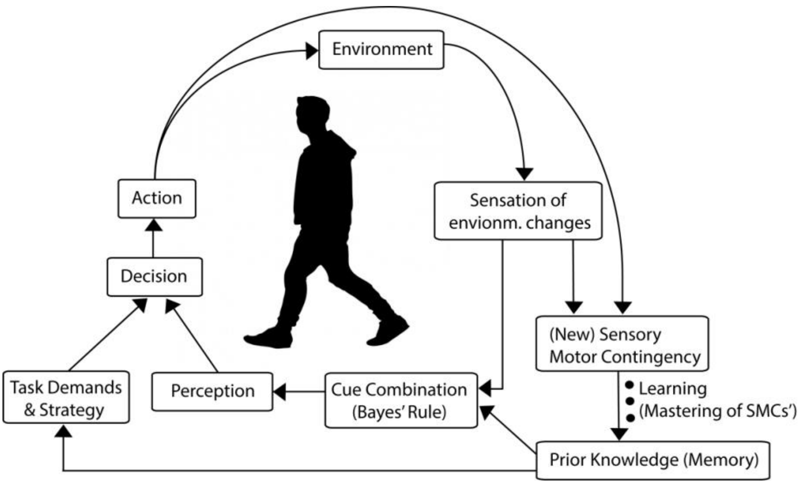

Figure 9: A combined model of sensorimotor contingencies and Bayesian cue integration. For an explanation refer to the text.

To test and verify such an action-oriented perspective of the human mind, it is of crucial importance to develop interactive experimental setups, which introduce and test action-perception associations. We followed such an approach in three of my studies. Most directly, we tested the theory of SMCs in the feelSpace study. Here the main research question was to find out whether humans can learn new SMCs based on an augmented sense. Emphasizing the importance of actions, both the learning phase and some of the behavioral tests (i.e. homing paradigm) took place in the real world (König et al., in press). Using the same augmentation device, in the platform study we investigated cue combination between native and augmented signals in untrained adults (no prior SMC). To create the new sensory-motor coupling, we build a platform that actively rotated (Goeke et al., 2016). In other words, the association between the augmented and the native cue was established by moving the participants around the yaw axis in the real world. Finally, in the alignment study we investigated how absolute and relative spatial information is stored in memory and how fast it can be accessed (Goeke et al., submitted). The proposed object-to-object spatial relations can well be interpreted as SMCs since they presumably represent or contribute to the knowledge of how to go from one object to another. Although the task itself was performed in the lab, we used real-world stimuli and hence the conclusions of this study are valid not only for an artificial, lab-based scenario, but especially for real world spatial navigation. In summary, the results of the alignment study, the feelSpace study and the platform study, fit nicely into a combined model of sensorimotor contingencies and Bayesian cue integration as outlined in Figure 9. Moreover, the experimental setups of these three studies extend the traditional lab-based testing approach such that the results are more directly transferable to the real world. As an overall conclusion, I can say that the final goal of my research is to develop a better and a more general understanding of the human mind, which is also valid outside the lab. Hence, I strongly believe that the only way to truly understand spatial cognition, multimodal processing, decision making, and other complex cognitive functions is to study the interactive nature of action and perception in a real world environment.

2. Study One: The First Online Navigation Study

This study has been published in “Frontiers in Behavioral Neuroscience”

Different strategies for spatial updating in yaw and pitch path integration

Goeke, C.M., König, P., & Gramann, K. (2013)

2.1 Abstract

Research in spatial navigation revealed the existence of discrete strategies defined by the use of distinct reference frames during virtual path integration. The present study investigated the distribution of these navigation strategies as a function of gender, video gaming experience, and self-estimates of spatial navigation abilities in a population of 300 subjects. Participants watched videos of virtual passages through a star-field with one turn in either the horizontal (yaw) or the vertical (pitch) axis. At the end of a passage they selected one out of four homing arrows to indicate the initial starting location. To solve the task, participants could employ two discrete strategies, navigating within either an egocentric or an allocentric reference frame. The majority of valid subjects (232/260) consistently used the same strategy in more than 75% of all trials. With that approach 33.1% of all participants were classified as Turners (using an egocentric reference frame on both axes) and 46.5% as Non-turners (using an allocentric reference frame on both axes). 9.2% of all participants consistently used an egocentric reference frame in the yaw plane but an allocentric reference frame in the pitch plane (Switcher). Investigating the influence of gender on navigation strategies revealed that females predominantly used the Non-turner strategy while males used both the Turner and the Non-turner strategy with comparable probabilities. Other than expected, video gaming experience did not influence strategy use. Based on a strong quantitative basis with the sample size about an order of magnitude larger than in typical psychophysical studies these results demonstrate that most people reliably use one out of three possible navigation strategies (Turners, Non-turners, Switchers) for spatial updating and provides a sound estimate of how those strategies are distributed within the general population.

2.2 Introduction

Spatial orientation is a fundamental and complex cognitive process associated with nearly every movement of the human body in the environment. While most people manage navigational tasks without even consciously thinking about it, the underlying neuronal and cognitive mechanisms are poorly understood. Spatial navigation relies on using and integrating sensory information from different modalities (Berthoz & Viaud-Delmon, 1999; Rossier, Haeberli, & Schenk, 2000). However, different modalities initially encode their information based on different reference frames, with each reference frame providing its own coordinate system (Soechting & Flanders, 1992). There are at least two distinct frames of reference, namely the egocentric and the allocentric reference frame (Kolb, Sutherland, & Whishaw, 1983). While the egocentric coordinate system is located within the agent and is contingent upon his orientation in space, the allocentric coordinate system decribes relations between objects, independent of the observers orientation (R. Klatzky, 1998). A spatial representation is then defined by a particular instantiation of reference frame use dependent on the task or environment. Redish and Touretzky proposed a model for animal navigation that included four different spatial representations; two of them are based on an egocentric reference frame, the other two on an allocentric reference frame (Redish & Touretzky, 1997). Human navigation might be governed by an interaction of various representations that are based on different frames of reference. Although humans are in general capable of using both reference frames, in most situations a preference to use either an egocentric or an allocentric strategy can be observed.

Spatial strategies, i.e., the use of a specific reference frame or the combination of different reference frames to solve a spatial task are thus to a large extend influenced by individual reference frame proclivities (Gramann, 2013). To illustrate this, let us consider the following example: you are visiting an unknown city looking on a city map in order to find your way. However, the map is not aligned with your current heading. In this situation you have at least two options to align your (egocentric) physical heading with the (allocentric) orientation of the map. First, you could rotate the map until it is aligned with your physical heading. Alternatively, you could mentally rotate until your imagined heading matches the orientation of the map. Why do some people turn the map while others mentally rotate and which cognitive mechanisms can be inferred from such behavior? Turning the map reflects a translation of the coordinate system of the map to match the egocentric coordinate system of the navigator's physical structure. Mentally rotating the navigator's heading reflects an adaptation to the allocentric coordinate system of the map. In other words, while one group of people prefers to compute spatial actions aligned with and based on their actual physical heading, another group prefers to compute spatial actions aligned with and based on a world-centered reference frame.

A promising way of investigating the cognitive basis for such differences in human behavior are virtual reality (VR) environments in which participants are free to use different reference frames when confronted with spatial tasks. Importantly, VR setups allow for precise experimental control. However, in typical desktop VR experiments, participants are not able to actively move and therefore lack embodied (proprioceptive and vestibular) cues. The absence of idiothetic information in VR experiments is associated with pronounced differences in spatial orientation strategies reflecting individual proclivities to use allocentric or egocentric reference frames (Gramann, 2013; Riecke, 2008). In particular, Gramann and colleagues demonstrated striking differences in the participants' responses when adjusting homing vectors after passages through virtual tunnels (Gramann et al., 2010, 2005, 2006).

In the categorization phase of this so-called "tunnel paradigm" participants saw virtual passages through tunnels with one turn to either the left or right side. At the end of a passage participants were ask to choose one out of two possible homing arrows to indicate their initial starting position at the beginning of the passage. Notably, one arrow indicated the direction toward the starting position based on an egocentric reference frame, corresponding to a change in cognitive heading during the turn. The other arrow indicated the homing direction based on an allocentric reference frame, corresponding to an unchanged cognitive heading aligned with the actual physical heading of participants. About half of the subjects preferred the egocentric homing arrow, while the other half preferred the allocentric homing arrow. However, the sample population was quite small and it remained unclear why participants used different reference frames for their responses.

Such differences in homing responses can be explained by individual proclivities to use different reference frames. However, Riecke and colleagues argue that the Non-turner behavior might be explained by simple left-right mirrored responses (Riecke, 2008). These studies however use a restricted range of path layouts. To systematically address this question in a recent study, Riecke (2012) used a wide range of path layouts confirming that differences in homing responses are based on a failure to integrate visually presented turns rather than due to “left-right mirrored responses.” Furthermore, accumulation of errors during the path integration process might contribute to behavioral differences if the error was systematic. Errors in the representation of the traversed path might be a result of incorrect encoding of the path or, alternatively, errors might result from an incorrect computation of a homing response based on a correct spatial representation. Fujita et al. (Fujita, Klatzky, Loomis, & Golledge, 1993) proposed the encoding error model that is based on configural updating of spatial information. This model assumes that people encode an internal representation of the pathway, rather than a homeward trajectory. As a consequence, homing accuracy is proposed to decrease and reaction times to increase with increasing complexity of the path. While this might be true the model does not account for the systematic individual differences reported in earlier studies including more complex path layouts (Gramann et al., 2005; Plank et al., 2010). Other researchers suggested continuous updating models (Wiener & Mallot, 2006) in which navigators continuously calculate a homing vector. This is in line with findings of Gramann and colleagues (Gramann et al., 2010, 2006) demonstrating that participants with distinct reference frame proclivities reveal differential neural activity already during the turning segment of the tunnel task. However, both the continuous and the configural model have difficulties in explaining the brain dynamic patterns and the performance differences of Turners and Non-turners in previous studies and future studies have to systematically address how the Turner and Non-turner behavior is connected to path integration strategies. The present study was designed to first investigate whether the individual differences in previous studies can be replicated for a large population. If this is the case, future studies can address the possible relationships of reference frame proclivities and underlying spatial updating processes.

Here we aimed at investigating how differences in strategy use are distributed in the overall population and which factors contribute to individual reference frame proclivities in a path integration paradigm. To this end, we analyzed data from a large number of participants to test whether previous findings on individual reference frame proclivities can be observed in a wider population and how such proclivities are distributed. Recently, the two main spatial strategies were replicated using a VR star-field task including horizontal (yaw) and vertical (pitch) rotation changes (Gramann et al., 2012). Besides two groups of Turner participants using an egocentric reference frame and Nonturner participants using an allocentric reference frame, some participants systematically switched from an egocentric reference frame for yaw rotations to an allocentric reference frame for pitch rotations. In the current investigation we thus included yaw and pitch rotations to further investigate whether this switching behavior can be replicated in a larger population. Moreover, we wanted to examine how stable reference frame proclivities are for individual participants and which factors potentially influence reference frame proclivities in the general population. In particular, we were interested how gender, video gaming experience, and self-estimated navigation abilities vary across strategy groups.

Gender differences are commonly proposed in navigation research. Most researchers agree that men outperform women on typical paper-and-pencil tests, or virtual navigation tasks that are based on geometric information (Moffat et al., 1998; Newhouse et al., 2007). Lawton (1994, 1996) evaluated self-reports of men and women and concluded that female participants less often use an allocentric strategy. Miller and Santoni (1986) and Dabbs et al. (Dabbs et al., 1998) showed that females base their navigation decisions more on landmarks or egocentric information. Furthermore, it has been suggested that females perform worse when using allocentric-based strategies (Astur et al., 1998; Rizk-Jackson et al., 2006; Sandstrom et al., 1998; Saucier et al., 2002). Overall, the general consensus is that males show better performance and use more often allocentric strategies than females during navigation (Woolley et al., 2010) However, recently van Gerven et al. (van Gerven, Schneider, Wuitchik, & Skelton, 2012) reported that when females are free to choose, they use allocentric strategies at least as often as males do, although using an egocentric strategy yielded to better performance. In order to shed more light on the issue, we aimed at investigating whether spatial reference frame proclivities differ between men and women selected from a large population.

Besides gender differences, recent studies imply an influence of video gaming experience on spatial cognitive processing. Most experiments focused on a correlation of video gaming experience and performance concluding that high video gaming experience leads to higher performance in navigational tasks (Frey, Hartig, Ketzel, Zinkernagel, & Moosbrugger, 2007; Richardson, Powers, & Bousquet, 2011). Moreover, Smith and Du'Mont (2009) demonstrated that self-estimated video gaming experience is correlated with performance in virtual navigation tasks. However, as there is no direct evidence that video gaming experience influences the use of distinct spatial reference frames, we included a gaming-related questionnaire to get individual estimates of video gaming experience that further could be used to correlate with individual navigation strategies.

Several studies have shown that self-estimates of spatial abilities predict navigation performance reasonably well (Gluck & Fitting, 2003; Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002). To allow for analyzing the influence of self-estimates of spatial abilities on navigation strategies, we included two additional questions regarding selfestimated navigation abilities; the first question referred to the ability to use cardinal directions, the second to general navigation skills. Moreover, we recorded decision certainty with respect to participants' performance hypothesizing that self-estimated spatial navigation skills and decision certainty are more pronounced when participants demonstrated a clear and stable strategy compared to people that randomly applied different strategies. Furthermore, we aimed at investigating whether selfestimated navigation abilities and decision certainty vary between participants preferring different reference frames for navigation. In general, the correlation of objectively measured responses and subjective assessments is a quite promising approach and offers several benefits. Namely, existing variations in the subjective experience of participants can be understood and possibly related to observed differences in navigation behavior. These insights might thereby also be helpful to develop new technologies for the diagnosis or treatment of patients with impaired spatial abilities

2.3 Methods

Online Study

The experiment was designed as an online study. The URL to the study was "www.navigationexperiments.com/TurningStudy. html." The main reason for designing an online study was the requirement for a large number of participants that could be best achieved through the internet. We advertized the online study on several web portals (e.g., Facebook, university homepage, etc.). Furthermore, we used existing scientific networks and contacted colleagues located in the US, Europe, and Asia to help acquiring participants. Therefore, we translated the webpage into six different languages (English, French, Spanish, Portuguese, German, and Russian). All participants performed the experiment independently on their own with detailed instructions given during the procedure. The homepage itself was programmed in HTML, Java Script, and CSS. The only requirement was that all participants used the latest version of Adobe's Flash player.

Path Integration Task

The main purpose of the study was to investigate strategy differences in virtual path integration. Following the idea of the tunnel paradigm, participants saw videos of passages through a dot cloud (**Figure 1A**). Every passage consisted of a first straight segment followed by one rotation (stimulus turn) to the left/right for yaw trials or up/down for pitch trials. After the stimulus turn a second straight segment followed after which the passage ended. The videos were created using "Vizard 3.0®," converted into .mp4 format and displayed with "Flowplayer 3.2®." The different segments smoothly transitioned and one passage including all three segments (first straight segment, stimulus turn, last straight segment) was perceived as continuous visual flow. Altogether three different angels (30, 60, and 90◦) and four different directions (up, down, left, and right) were realized, adding up to 12 different passages. Each passage was presented twice such that all participants watched 24 videos in a randomized order. At the end of a passage four homing arrows appeared pointing into different directions (**Figure 1B**). Two out of the four displayed homing arrows were considered correct. Both indicated the exact direction in three dimensional space toward the starting location dependent on the path traversed. The orientations of the displayed homing arrows dependent on the angle of rotation during the passage such that passages with acute angled turns resulted in homing arrows pointing more inward than passages with less acute turning angles. However, one arrow pointed back in accordance to an allocentric reference frame while the other was in accordance to an egocentric reference frame. Choosing either of the other two arrows was considered as an erroneous response. For example, after a passage with a rotation in the yaw plane the two homing arrows pointing back-left or to back-right were considered correct (**Figures 1C,D**), while the two homing arrows pointing back-up or pointing back-down were considered incorrect (and vice versa for pitch rotations). Participants were then asked to select one out of the four homing arrows to indicate the direction toward the starting position. This was done by clicking on the respective arrow with a computer mouse. We measured response type (egocentric, allocentric, or incorrect) and reaction time. Reaction time was defined as the time from onset of the arrow selection screen until the participant clicked on one of the arrows. This was done with a Java Script file running on the client PC, which ensured that there was no bias from internet connection. Inter-trial time was not recorded as it was heavily biased by the speed of the individual internet connection. Subjects were instructed to start the experiment only when sufficient time was at hand to perform it in a single session. In that case the experiment took about 15–20 min in total. Before the experiment started all subjects were informed about the task and instructed to focus during the whole experiment and not take any breaks (see appendix for the instructions). After participants navigated through all passages they filled out a questionnaire asking for gender, age, gaming and computer experience, decision certainty, and self-estimated navigation skills (see Appendix for the complete questionnaire).

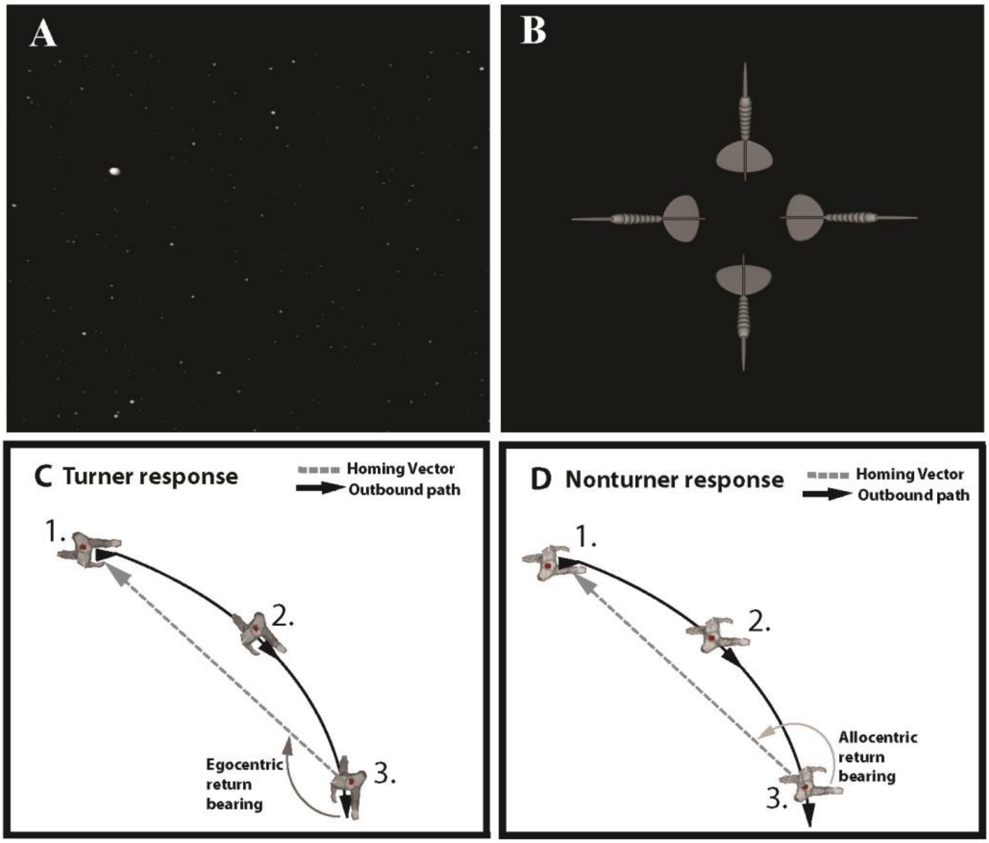

FIGURE 1 | Experimental paradigm. (A) Snapshot of the star-field passage in the experiment. During the passage the white dots (stars)-induced visual flow indicating a turn into one direction. **(B)** Forced choice arrow selection in the experiment. After a 90◦ rightward turn. The arrow pointing to the right indicates the homing vector in line with an egocentric reference frame; the arrow pointing to the left is congruent with an underlying allocentric reference frame. Choosing one of the other two arrows (up and down in this case) was counted as incorrect response. (C,D) Turner and Non-turner responses respectively in a schematic drawing of a 90◦ rightward turn from a bird's eye view. The curved black line indicates the turn of the virtual passage. (1) Before the turn both strategy groups Turners (panel **C**) and Non-turners (panel **D**) have an identical heading. (2) While the cognitive heading of Non-turners does not change during the stimulus turn, Turners adapt their cognitive heading according to the degree of the stimulus turn. (3) At the end of the passage after the turn, Turners base their response on the cognitive heading aligned with the virtual environment and therefore point to their right and back (egocentric bearing return). Non-turners respond based on a cognitive heading that is still aligned with their physical heading and thus point to their left and back (Allocentric return bearing).

Participants

Data from 300 participants was recorded. Six subjects were excluded as they had missing data in the questionnaire. Initially, we analyzed the distribution of incorrect responses. Most subjects did not commit any error but some subjects responded incorrectly in more than half of the trials indicating complete spatial disorientation or a lack of attention during the task. Because we wanted to investigate homing adjustments in participants that were oriented during the task, we excluded subjects with too many incorrect responses. The distribution of incorrect responses showed a natural inflection point at 2–3 incorrect responses and we thus removed subjects with more than 2 incorrect responses (n = 34) from further analyses. This resulted in 260 participants with nearly an even split of male (132) and female (128) participants. Most participants were university students with an average age of 27.14 years (SD = 9.83 years) living in more than 15 different countries. Cultural impact on spatial navigation was not analyzed due to the relatively sparse distribution (most participants lived in Germany or Spain). In total, 24 of all 260 participants were left handed. No participant received reimbursement for the experiment but all participants were offered information on their preferred spatial strategy at the end of the experiment.

Correlation of Behavioral and Questionnaire Data

We preprocessed questionnaire data dependent on data scaling; dichotomous variables were dummy coded and variables that used a Likert Scale were normalized and then z-transformed. (See appendix for the complete questionnaire). Overall we investigate the correlation of preferred spatial strategy with the factors: gender, video gaming experience, sense of direction, general navigation self-estimation, and decision certainty. As the study was conducted online, we did not include a complete spatial navigation questionnaire (e.g., Santa Barbara Sense of Direction Scale) because it would have taken much time and some subjects presumably would have left the page without filling out the complete questionnaire. Hence, we included only 2 questions. One question was targeting allocentric (cardinal direction) navigation performance and another question was targeting general navigation performance (see appendix for whole questionnaire). For video gaming experience we combined the responses of five questions into one final estimate for each subject. Since the different sub-scales included different scaling, all variables were first normalized and then a PCA was computed to reduce dimensionality. The z-transformed value of the first principle component was finally used for the analysis of video gaming experience.

Discriminant analysis

Strategy was analyzed by discriminant analysis as a function of the following factors: gender, self-estimated video gaming experience, self-estimated ability to use cardinal directions, self-estimated general navigation skill, and decision certainty. Other factors like age or handedness could not be included due to sparseness or rareness. In order to identify which combination of individual factors distinguished the strategy groups best, we calculated the structure matrix of the discriminant functions. Because the dependent variable (strategy use) had four levels (Turner, Non-turner, Switcher, No Preference) the discriminant analysis computed 3 different discriminant functions, providing a weighted combination of the independent variables that led to the maximal separation of the four levels of the dependent variable. Finally, we tested each discriminant function for significance.

Analysis of variance

The discriminant analysis provided us with a linear combination of individual factors that discriminated between strategy groups. Wilks' Lambda was computed to test for significance of the individual variables. Additionally, we inverted the analysis using gender, gaming experience etc., as the dependent variable and strategy group as the independent variable. With that approach we were able to apply an analysis of variance with pairwise comparisons in order to investigate the exact difference of these factors between the strategy groups.

Classification

The final step in the analysis was to predict strategy based on the questionnaire data. First, we used the discriminant functions for classification. Such generative models are well-suited since they describe the relationship between the predictor variables and different groups of the dependent variable. A second approach was to use a Support Vector Machine (SVM) instead of discriminant functions. The advantage is that a SVM can also calculate non-linear relationships and use those weights for later classification. In both methods we used cross validation to estimate prediction accuracy.

2.4 Results

Response Behavior

First we analyzed the distribution of response types over the course of the experiment, investigating whether strategy-specific responses occurred more often in the beginning of the experiment as compared to later trials or vice versa. The relative amount of each response type over trials was then fitted with a linear regression and the slopes of the regression lines were tested in an F-test against the zero hypotheses of zero slope. We observed a stable distribution of allocentric, egocentric, and incorrect responses for both axes over the course of the experiment (**Figure 2D**). All slopes of the linear regression curves did not significantly differ from zero ($p > 0.05$) for any response type.

Due to the nature of the online experiment we took additional measures to ensure that only trials entered further analysis where participants likely attended to the task and successfully kept up spatial orientation. First, a Two Way ANOVA with factors axis (yaw and pitch) and response type (egocentric, allocentric, and incorrect) was computed to uncover potential differences in response latencies. The analysis revealed a significant influence of the factor response type [$F(1, 765) = 12.98$; $p < 0.01$] but not for the factor axis [$F(1, 765) = 0.68$; $p > 0.1$] or an interaction of both factors [$F(1, 765) = 2.17$; $p > 0.1$; **Figure 2C**]. An additional pairwise comparison demonstrated that incorrect responses had significantly higher response latencies than both egocentric and allocentric responses [$F(2, 765) = 40.39$; $p < 0.01$]. As this shows that incorrect responses were somehow different from correct responses, we did not analyze incorrect trails for the rest of the analysis.

As incorrect responses were not considered further, the amount of allocentric responses was the inverse of the amount of egocentric responses. In a next step we analyzed the ratio of allocentric and egocentric responses for different passages. In order to be able to perform statistical analysis, we separated the data into 10 groups of 26 participants each. For each of these groups we then calculated the mean (egocentric vs. allocentric) response ratio for different passages. An ANOVA with factors angle (30, 60, and 90◦), axis (yaw, pitch) and order (first or second presentation) investigated the difference in response type (allocentric vs. egocentric). The analysis revealed a significant main effect for the factor axis [$F(1, 108) = 74.2$, $p < 0.001$] but no effect for the factor angle [$F(2, 108) = 2.55$, $p = 0.0831$] and the factor order [$F(1, 108) = 1.56$, $p > 0.1$]. Furthermore, none of the interactions reached significance. Comparing **Figures 2A** (pitch) and **B** (yaw) demonstrates that participants used the allocentric strategy more often in pitch than in yaw passages. This result underlines that reference frame proclivities are dependent on the environment, i.e., the axis of rotation. On that account, passages with different angles and directions were aggregated and only the factor axis (yaw vs. pitch) was considered for further analyses. This way the number of different response types was reduced to four (egocentric yaw, allocentric yaw, egocentric pitch, allocentric pitch).

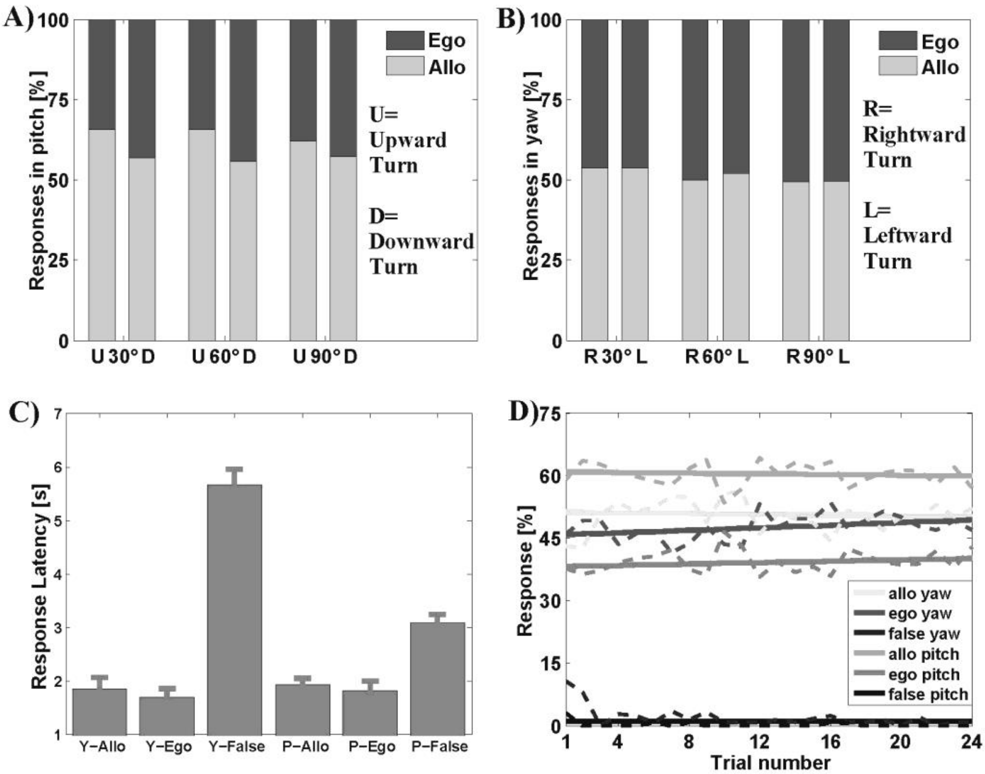

FIGURE 2 | Investigation of response types. (A,B) Ratio of allocentric vs. egocentric responses for all passages in pitch (panel **A**) and yaw (panel **B**). In both figures the y-axes displays the relative amount of allocentric vs. egocentric responses. The x-axes indicate the different passages in both yaw and pitch. The dark gray bars indicate the amount of egocentric responses; the light gray bars indicate the amount of allocentric responses. (**C**) Response times for all responses types. The y-axis shows the response times in seconds from stimulus onset (appearance of the arrows) until one arrow was chosen (mouse click). The x-axis shows the various response types (allocentric, egocentric, and incorrect) separately for both axes (Y stands for yaw and P for pitch; False stands for incorrect). The gray bars indicate the means and standard errors of response times for each response type. (**D**) Distribution of response types over trials. The y-axis displays the relative amount for all response types. The x-axis shows the trial number. Each line represents the relative amount of the respective response type for each trial in yaw or pitch. The dotted lines display the actual data and the solid lines show the linear regression fits.

Reference Frame Proclivities

After we performed all the necessary preprocessing steps we investigated how stable reference frame proclivities were on an individual basis. As the histogram in **Figure 3A** shows, most participants exclusively chose either an allocentric homing arrow (rightmost bar) or exclusively an egocentric homing arrow (leftmost bar) in yaw trials. We observed a similar pattern for pitch trials (**Figure 3B**). As each passage was displayed twice, we compared reference frame proclivity for the first and second response of each passage. Hence the Pearson product-moment correlation coefficient r was calculated for both yaw ($r = 0.9563$) and pitch ($r = 0.9166$) trials. The correlations were significant for both axes ($p < 0.001$). Moreover we also calculated the correlation between yaw and pitch responses with respect to reference frame proclivity. Again the Pearson product-moment correlation coefficient ($r = 0.81$) revealed significance ($p < 0.001$). These data indicate that participants responded consistently with clear preferences throughout and that reference frame proclivity did not change over time.

Strategy Formation

The key interest in the present study was to evaluate the distribution of navigation strategies in the overall population. In order to make a more general statement about individual strategy use, the data was synthesized with respect to the overall response pattern in yaw and pitch axes simultaneously. Most participants demonstrated a clear and stable navigation strategy, as reflected in two clusters in the lower left and the upper right corner (**Figure 3C**). Only few participants were located in the center of the distribution, showing no preference in reference frame use. Instead the peaks of the clusters were located on the edges of the distribution, reflecting the fact that most participants exclusively chose either an egocentric or an allocentric reference frame for both yaw and pitch rotations.

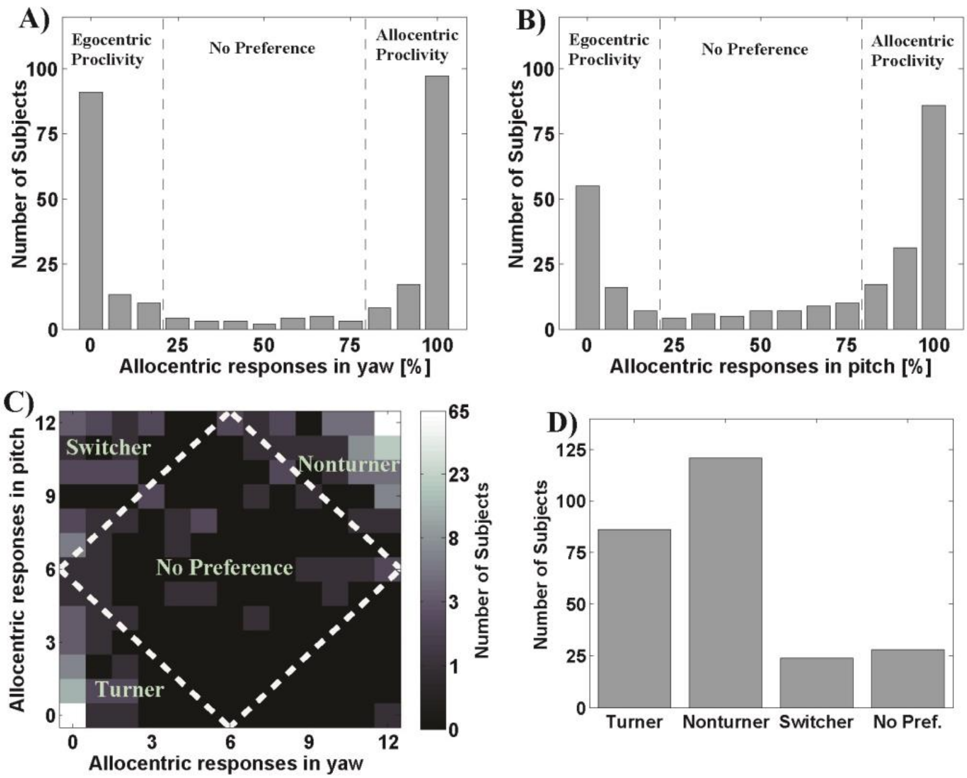

FIGURE 3 | Response distribution and strategy formation. (A,B) Histograms of responses for yaw (panel **A**) and pitch (panel **B**) rotations. In both figures the y-axes indicate the number of subjects. The x-axes show the amount of allocentric responses. The height of the gray bars indicates the amount of subjects for each ratio of allocentric vs. egocentric responses (0 means all responses were given using and egocentric reference frame; 100 means all responses were given using an allocentric reference frame). The black dashed lines indicate the boundaries that were later on used to group people into different strategy classes. (**C**) Combined response pattern for all subjects indicating strategy class. The y-axis indicates the amount of allocentric responses in pitch, the x-axes indicates the amount of allocentric responses in yaw. The brightness of the squares reflects the amount of subjects that have the identical ratio of allocentric vs. egocentric responses for both yaw and pitch (bright colors indicate many subjects; dark colors few subjects). The logarithmic scale to the right shows the amount of subjects corresponding to each level of luminance, with rounded values. The white dashed line marks the boundaries between the strategy groups. Additionally, the labels indicate the names for the strategy groups. (**D**) Strategy distribution in the overall population. The y-axis indicates the amount of subjects; the x-axis indicates the different strategy groups. The height of the gray bars indicates the amount of subjects belonging to a particular strategy group.

We classified all subjects into one of five strategy groups using the factors reference frame proclivity (egocentric vs. allocentric) and axis (yaw vs. pitch). Participants who used an egocentric reference frame in at least 19 out of trial 24 trials (>75%) were classified as Turners, while participants using an allocentric reference frame in at least 19 out of 24 trials (>75%) were classified as Non-turners (for a detailed discussion on the nomenclature see Gramann et al., 2012). In addition, participants could switch between reference frames dependent on the axis of rotation. In theory two scenarios were possible: Participants could switch from an egocentric reference frame in yaw to an allocentric reference frame in pitch or, vice versa, participants could switch from an allocentric reference frame in yaw to an egocentric reference frame in pitch. Participants adopting a yaw-ego pitch-allo strategy in at least 19 out of 24 trials were classified as Switchers, while participants adopting a yaw-allo pitch-ego strategy were classified as Inverse Switchers. However, as only one subject adopted the latter strategy we did not further investigate this behavior. The remaining participants revealing no clear reference frame proclivity were assigned to the No Preference group. This classification scheme conforms to the use in previous experiments (Gramann et al., 2010, 2012).

Finally, we calculated the number of participants in each strategy group. As shown in **Figure 3D**, 33.1% (86 subjects) were classified as Turners (egocentric reference frame proclivity for both axes), 46.5% (121 subjects) as Non-turners (allocentric reference frame proclivity for both axes). Furthermore 9.2% (24 subjects) consistently switched between an egocentric reference frame in yaw and an allocentric reference frame in pitch. However, the reverse assignment was rarely observed and only a single participant switched consistently between an allocentric reference frame in yaw and an egocentric reference frame in pitch. Hence this subject is not considered in further analysis while participants consistently switching from egocentric in yaw to allocentric in pitch were now labeled Switcher. In total, 10.8% (28 subjects) did not show a strategy preference. These data show that the overwhelming part of subjects responded consistently using either the Turner, Switcher, or Non-turner strategy.

Response Latencies

In a next step we analyzed response latency as a function strategy and consistency. In particular, we wanted to know first whether different strategy groups answered faster or slower than others and second whether trials in line with the overall preference of a subject have a shorter reaction time than trials that were not. To this end, we separated all participants into 10 groups with 26 participants each. For each of these groups we divided the data according to the two factors of interest, i.e., strategy use and consistency. As for subjects in the no-preference group a separation of consistent and inconsistent trials is not possible, we visualized results of these subjects but excluded them from the statistical analysis. Next we calculated the median response time pooled over subjects within each group but separately for each combination of conditions. This resulted in 10 (groups) × 3 (strategy use) × 2 (consistency) values. As the median is a robust estimator of central tendency, this procedure ensured that outliers did not influence the results. **Figure 4A** visualizes the mean of the 10 groups, separately for each condition also including the no-preference group. The figure shows pronounced differences between consistent and inconsistent responses for all strategy groups. Moreover, average reaction times in the no preference group are more similar to inconsistent than to consistent responses of the other strategy groups. Finally, we performed a Two Way ANOVA with the factors strategy and consistency as independent variables and reaction time as the dependent variable. In order to avoid a bias from the initial splitting of subjects into the 10 different groups and to provide more robust statistics, we iteratively tested 10,000 different splittings of subjects and gathered the distribution of p-values from the subsequent ANOVAs. For the factor consistency all p-values were below 0.05 and 97.89% were below 0.01 showing that consistent responses were significantly faster than inconsistent responses. No other factor or interaction reached significance (in both cases 98% of p-values failed to reach $p < 0.05$). Representative One-Way ANOVAs revealed a significant effect of consistency for all strategy groups [Turners: $F(1, 19) = 7.85$, $p < 0.05$, Nonturners: $F(1, 19) = 23.91$, $p < 0.01$, and Switchers: $F(1, 19) = 4.74$; $p < 0.05$]. These results support the assumption that Switchers indeed constitute a strategy group separate from Turners and Non-turners. Furthermore, these results further support the hypothesis that the use of a non-preferred spatial reference frame is associated with different cognitive processes that are likely computationally more demanding.

Strategy and Self-Assessment

Variations in navigation behavior were most prominent between but not within subjects. To uncover this disparity we performed a discriminant analysis and consequently calculated the structure matrix as shown in **Table 1**. The analysis revealed that the first discriminant function significantly differentiated between the strategy groups (df = 12, Wilks' Lambda = 0.816, $p < 0.001$), while the second discriminant function was borderline significant (df = 6, Wilks' Lambda = 0.954, $p = 0.062$). The third discriminant function did not help differentiating strategy groups (df = 2, Wilks' Lambda = 0.999, $p > 0.1$). The first function was mostly dependent on decision certainty and cardinal direction proficiency, while the second function was mostly dependent on gender and video gaming experience. Furthermore, we investigated significance of the single variables using Wilk's Lambda in an ANOVA F-test. The result showed that gender, cardinal direction proficiency, and decision certainty significantly contributed to the discrimination of the strategy groups ($p < 0.05$). However, to gain more insight about the relation of the predictor variables and the strategy groups we analyzed whether the values of the predictor variables were significantly different between the strategy groups. The analysis of gender (**Figure 4B)** revealed that females were predominantly Non-turners (54.7%) as compared to Turners (26.6%), while males used both the Turner (39.4%) and the Non-turner (38.6%) strategy more or less evenly distributed. Furthermore, males were more likely to be Switchers (12.9%) than females (5.5%). Overall, Turners had the highest decision certainty followed by Non-turners, Switchers, and finally participants with no reference frame preference (**Figure 4C**). A pairwise-comparison revealed a significant difference between Turners and Non-turners compared to subjects with no strategy preference [$F(3, 258) = 14.05$, $p < 0.001$]. The self-estimated ability to use cardinal directions revealed a similar pattern as decision certainty. Turners revealed the highest confidence in their ability of cardinal direction use and participants without strategy preference were most unconfident using cardinal directions. Again a paired comparison revealed significant differences between Turners and Non-turners compared to subjects without preference. [$F(3, 258) = 3.49$, $p < 0.05$, **Figure 4D**]. Surprisingly, self-estimated general navigation skills did not show any difference between strategy groups [$F(3, 258) = 1.19$, $p > 0.1$; **Figure 4E**]. Although there is a trend that video gaming experience differentially affected strategy use for males and females the ANOVA revealed that video gaming experience neither directly [$F(3, 258) = 2.05$, $p > 0.1$] nor via an interaction with gender-influenced strategy use [$F(19, 259) = 0.83$, $p > 0.1$; Figure 4F].

Predictor Variable/ Discriminant Function	**Function 1***	**Function 2**	**Function 3**
Decision Certainty	**.970**	-.002	.150
Cardinal Direction Ability	**.466**	-.242	-.146
Gender	-.183	**.951**	.170
Gaming Experience	.118	**-.668**	.307
Navigation Skill	.222	-.261	**.784**

Table 1 | Structure Matrix of Discriminant Functions. The first column indicates the name of the predictor variable. The second to forth column show the structure coefficients for the three different discriminant functions. The values in bold depict the highest correlation of a certain predictor variable with a certain discriminant function. The asterisk indicates significance of the discriminant function.

Strategy Prediction

Applying results of the previous section we investigated in how far the chosen strategy can be predicted based on the self-assessment. Predicting individual reference frame proclivity separately for both axes using a SVM reached 62.38% in yaw and 67.54% in pitch, compared to a chance level of 50%. Predicting complete strategy groups in 3D space (in Turner, Switcher, Non-turner, and inconsistent groups) using discriminant functions, classification performance was above chance (25%) at a level of 42.1% correct classifications. SVM classification improved this result to a correct classification rate of 54.36%. These data demonstrate that the chosen strategy can be predicted based on the self-assessment at a moderate level.

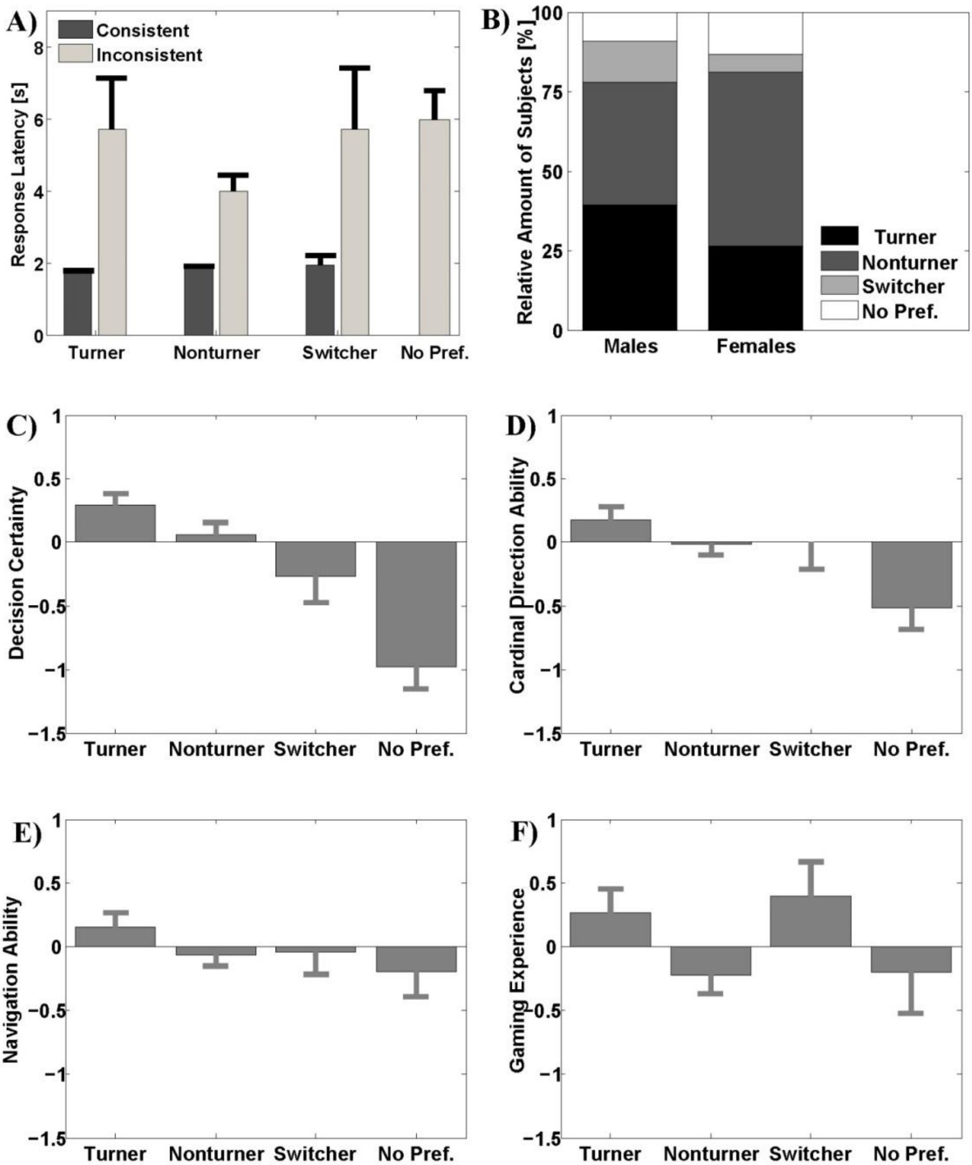

FIGURE 4 | Subgroup investigations (A) Response latency for strategy groups. The y-axis indicates the response time in seconds. The x-axis represents the four different strategy groups. The dark gray bars show the average response latency for responses inconsistent with the preferred strategy including standard errors; the light gray error bars show the average response latency for responses consistent with the preferred strategy; also including standard errors. (**B**) Distribution of strategy use for males and females. The y-axis indicates the relative amount of subjects belonging to a particular strategy group. The x-axis separates male and female participants. The stacked bar diagram shows the distribution of strategy groups for male and female subjects. The different shades of gray color-code the four different strategy groups. (**C,E**) Variations of self-assessed variables between strategy groups. The y-axes indicate the value of the self-estimated variable on a z-score scale. The x-axis separates the different strategy groups. The height of the gray bars indicates the mean value for the different strategy groups, including standard errors. Panel (**C**) displays Decision Certainty; panel (**D**) displays Cardinal Direction; panel (**E**) displays Navigation Skill; and panel (**F**) displays Gaming Experience.

2.5 Discussion

Here we investigated a large group of participants in a 3D virtual navigation task and found strong evidence that the majority of subjects reliably used a particular navigation strategy. More than 85% of the sample population demonstrated a clear and stable strategy in the experiment. Although most subjects preferred the same reference frame for both axes, we proofed the existence of a third distinct strategy group that systematically switched between reference frames from egocentric in yaw to allocentric in pitch. The opposite change of reference frame proclivities was rarely observed and did not represent an own strategy group. We conclude that there are three distinct spatial strategies (Turners, Non-turners, and Switchers) and that subjects reliably choose one spatial strategy for virtual navigation. These results support earlier findings concerning the use of distinct spatial strategies (Gramann, 2013; Gramann et al., 2010, 2005, 2006; Moffat, Zonderman, & Resnick, 2001; Riecke, 2008; Rodgers et al., 2012) Most importantly, we showed that the reported difference in strategy use is a general and remarkably prominent phenomenom in the overal population. To our understanding such strong distinctions during updating of spatial information in yaw and pitch navigation must be considered in future studies of spatial navigation.

Potential Restrictions of the Present Study

The experiment was conducted as an online study that is potentially associated with a number of issues. First, participants were not directly instructed and supervised by an experimenter. This opens the possibility that participants might not have understood the task or could have been distracted (people walking in the room, phone calls, etc.) during the experiment. However, instructions were given in detail on the webpage beforehand. Furthermore, it is reasonable to assume that participants who did not understand the task or were not concentrated during the experiment would have made many incorrect responses. However, most subjects had fast reaction times and did make few if any errors. Specifically, the few subjects with more than two errors were excluded from the analysis. Furthermore, the experiment was self-scheduled by the participants, favoring a timing-free of other constraints or tasks. Therefore, we can reasonably assume that all participants used in the analysis attentively carried out the task as would subjects under lab conditions.

Second, an online study does not control for the experimental environment during the task. Participants in this study presumably used different computers, monitors, and software (browser). However, we tested various browsers and monitors before starting the experiment and did not observe any crucial differences. Furthermore the position between the monitor and the participant might have varied between participants. However, we do not have any reason to assume that it conflicts with the classification schema (Turner, Non-turner, and Switcher) made in our paradigm. Furthermore, it is reasonable to assume that if the angle between monitor and participants varied that such a bias is normally distributed among the population (i.e., some people place it to their right, most in the center, some others to their left). Finally, there is no evidence suggesting that certain subgroups (e.g., males, females) have a preference for a particular option (monitor position). Overall it is to say that the task was relatively simple and we did not get any critical feedback about technical problems. Altogether we believe that the benefits of the online study outperformed the shortcomings by far.

Individual Differences Influencing Strategy Selection

A major result of the present study is a gender-specific difference in spatial strategies. Most former studies mentioned that males prefer allocentric navigation while women tend to use egocentric strategies (Lawton, 1994, 1996). However, van Gerven et al. (2012) recently proposed that women use allocentric strategies to a similar extent than males. This is supported and extended by our results demonstrating that the majority of women in our task prefer an allocentric navigation strategy and that more women than men prefer an allocentric over an egocentric navigation strategy. One might speculate why we found such differences while earlier studies did not? One reason might be that previous studies forced participants to use one or the other spatial strategy. Based on such instructions Sandstrom and colleagues come to the conclusion that women avoid allocentric strategies because their performance was impaired compared to egocentric strategies (Astur et al., 1998; Rizk-Jackson et al., 2006; Sandstrom et al., 1998; Saucier et al., 2002). This conclusion is at odds with the observed distribution of spatial strategies in a large population of participants. Furthermore, in our study, video gaming experience varied significantly between men and women; however it did not have a significant influence on strategy use. Therefore, the reported gender differences cannot be explained by different levels of experience with virtual environments. Richardson et al. (2011) and Frey et al. (2007) demonstrated that video gaming experience is highly correlated with performance in virtual navigation tasks. Here we investigated the influence of video gaming experience on the use of distinct spatial strategies. More specifically, we expected participants with a strong gaming background to be more easily immersed within the virtual environment and thereby to adopt an egocentric strategy. However, no such effect was observed. One explanation for the missing influence of video gaming experience on spatial strategies could be the experience with different types of computer games and the associated reference frames (e.g., 3D-first person vs. 2D-bird's eye view games). Conclusively, some video games favor an egocentric strategy while others favor an allocentric strategy. Hence, high video game experience could lead to different biases in strategy use depending on the type of game that individuals prefer. In order to determine the influence of video gaming experience on navigation strategies, future studies have to use extended questionnaires analyzing differences in reference frames used in specific video games. Finally, we observed significant variations between strategy groups for decision certainty and cardinal direction abilities. The fact that people with no reference frame proclivity were much less confident in their responses compared to Turners and Non-turners suggests that those subjects indeed did not follow a clear navigation strategy and therefore supports our categorization of strategy classes. Gluck and Fitting (2003) and Hegarty et al. (2002) reported that individual estimates of navigation abilities correlate with the observed performance in spatial tasks. Here we speculated that different levels of spatial performance correlate with the use of distinct reference frames. Although cardinal direction use implies an allocentric reference frame, we did not find differences between Turners and Non-turners but again between participants revealing a clear and stable navigation strategy as compared to participants who did not show any preference. In general, these results suggest that both Turners and Non-turners are able to use (allocentric) cardinal directions in the real world, while people without strategy preference are in general more challenged during spatial orienting.

Overall the influence of individual differences in established spatial measures on reference frame proclivities did not match all our hypotheses. In particular, it remains unclear which other important factors contribute to the general distinction between Turners and Non-turners. However, we have shown that a weighted linear combination of the variables gathered in this study is able to significantly discriminate between strategy groups and helps to predict strategy use up to a reasonable level. How such a reference frame proclivity observed in a VR setup is related to real world navigation remains speculative. In a current experiment we are investigating whether the strategy differences observable in virtual path integration also apply to real world navigation. In particular we are interested whether Non-turner responses are also present during real world navigation. However, the influence of reference frame proclivities might also be reflected in other ways. Potentially Turners tend to use well-known routes instead of computing detours in cases where this might be possible or Non-turners might prefer to communicate directions based on allocentric information (e.g., cardinal directions). Future research has to investigate these issues.

Reference Frame Proclivities in Yaw and Pitch

We provide evidence that reference frame proclivities in a virtual path integration paradigm are dependent on the specifics of the environment, i.e., the axis of rotation. However, the question remains, why some participants use such a Switcher strategy. Vidal et al. (Vidal, Amorim, & Berthoz, 2004) showed that performance in a path recognition paradigm was better in terrestrial navigation including only yaw rotations, compared to weightless navigation also including pitch rotations. Human navigation is innately specialized for terrestrial (horizontal) navigation and performance in pitch trials could be impaired because of two main factors (Gramann et al., 2012). First, yaw rotations have a higher ecological validity (we experience them more often in the real world) and second the conflict between vestibular and visual information is more pronounced in pitch as compared to yaw rotations. While for yaw trials there is (only) a mismatch in the rotation information in pitch trials there is an additional mismatch in with respect to gravitational forces (Gramann et al., 2012). Using a similar paradigm Gramann et al. (2012) found that both absolute pointing errors and pointing variability were only slightly increased in pitch trials as compared to yaw trials. However, in the current experiment participants used signifi- cantly more often the allocentric strategy in pitch compared to yaw trials. Arguably, a decrease in pitch performance, arising from an increased visuo-vestibular conflict, might be counterbalanced or avoided by a shift of reference frame use. Strong evidence for this assumption comes from participants preferring an egocentric reference frame in yaw but switched to an allocentric reference frame in pitch, but not vice versa. Divers, pilots, and certain athletes who are used to vertical head rotations provide a good opportunity in this respect for future research.

Summary

Altogether the present study provides strong evidence that humans have clear and stable reference frame proclivities for updating spatial information on a single axis. Differences in reference frame proclivities between both axes (yaw and pitch) are potentially related to the difference in the ecological validity of both kinds of rotations (horizontal vs. vertical). Individual responses based on the non-preferred reference frame with respect to participants' overall preference demonstrated prolonged response latencies, indicating differences and/or higher effort with respect to the underlying cognitive processes. Combining both yaw and pitch reference frame proclivities makes up three distinct and separable spatial strategies (Turners, Nonturners, and Switchers). More than 85% of participants reliably chose one of these strategies to solve the 3D path integration task. The fact that our study comprises data from 300 subjects renders it likely that the reported distribution of navigation strategies is a robust estimate of the true variation within the overall population. Contrary to earlier studies, we find that women prefer the Non-turner strategy that is based on an allocentric reference frame, while men do not show a preference between the Turner and the Non-turner strategy. Furthermore, we demonstrate that a linear combination of the variables gender, decision certainty, and cardinal direction proficiency can be used to discriminate strategy groups and also predict group membership to some degree. In future research, we aim to further investigate the influence of other factors, i.e., age and cultural background on reference frame proclivity to finally unravel the underlying factors determining human navigation strategies.

2.6 Acknowledgements

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3. Study Two: The Follow-Up Online Navigation Study

This study has been published in “Nature Scientific Reports”

Cultural background shapes spatial reference frame proclivity

Goeke, C., Kornpetpanee, S., Köster, M., Fernández-Revelles, A. B., Gramann, K., & König, P. (2015)

3.1 Abstract

Spatial navigation is an essential human skill that is influenced by several factors. The present study investigates how gender, age, and cultural background account for differences in reference frame proclivity and performance in a virtual navigation task. Using an online navigation study, we recorded reaction times, error rates (confusion of turning axis), and reference frame proclivity (egocentric vs. allocentric reference frame) of 1823 participants. Reaction times significantly varied with gender and age, but were only marginally influenced by the cultural background of participants. Error rates were in line with these results and exhibited a significant influence of gender and culture, but not age. Participants' cultural background significantly influenced reference frame selection; the majority of North-Americans preferred an allocentric strategy, while Latin-Americans preferred an egocentric navigation strategy. European and Asian groups were in between these two extremes. Neither the factor of age nor the factor of gender had a direct impact on participants' navigation strategies. The strong effects of cultural background on navigation strategies without the influence of gender or age underlines the importance of socialized spatial cognitive processes and argues for socio-economic analysis in studies investigating human navigation.

3.2 Introduction

Spatial navigation is a central human cognitive skill. Various scientific studies have concentrated on investigating differences in navigation performance and navigation strategies, in particular dividing egocentric and allocentric navigation. Navigation can be based on different reference frames using distinct coordinate systems to encode spatial information. An egocentric coordinate system is located within the agent and is conditioned upon his orientation in space, while an allocentric coordinate system codes relations between objects, independent of the observers' orientation (Klatzky, 1998). Several studies in spatial navigation demonstrated pronounced changes in spatial navigation performance in elderly participants (Lövdén et al., 2012). Comparisons of navigation performance in young and elderly participants revealed an age-based decline in speed and accuracy as well as changes in navigation strategy (Rodgers et al., 2012) and their underlying preference for using an egocentric or allocentric spatial reference frame. Changes in preference that lead to using an egocentric reference frame with older age might be directly related to changes in the neural substrate subserving computation of different reference frames. However, individual proclivities to use an egocentric or an allocentric reference frame can be observed already in young and middle-aged participants (Gramann et al., 2005; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). Considering such pronounced individual differences in the use of an egocentric or an allocentric reference frame, it is important to delineate the underlying mechanisms that shape the proclivity to use different reference frames. In this respect, Gramann and colleagues revealed specific cortical activation patterns to be associated with the use of particular reference frames (Gramann et al., 2010). Gramann argues that both types of reference frames (egocentric and allocentric) are soft-wired (genetically predetermined) on a neuronal level, but that several additional factors influence the development of individual reference frame proclivities (Gramann, 2013). A rough separation can be made between environmental and biological factors. On the one hand, the development of the physical structure (i.e., maturation) and motor skills (e.g. upright walking) impacts the neural circuitry underlying computation of a distinct reference frame. On the other hand, cultural factors like socioeconomic status, language, or urbanization strongly influence maturation of individual spatial reference frame proclivities (Haun, Rapold, Call, Janzen, & Levinson, 2006; Haun, Rapold, Janzen, & Levinson, 2011; Hoffman et al., 2011). This view is in line with other studies investigating individual differences in spatial cognitive abilities. Waller showed that gender, computer and navigation interface proficiency shape individual differences in navigation performance (Waller, 2000). Hegarty and colleagues performed structural equation modelling comparing a variety of spatial tasks and learning strategies, confirming that gender differences were present throughout most tasks that were considered (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). More recently, Wolbers & Hegarty summarized existing literature regarding individual differences in spatial cognition and concluded that human spatial navigation is influenced by a multitude of factors, including gender and age, but also the individual preference to use different environmental cues (Wolbers & Hegarty, 2010). In this light, the current study further investigates the underlying mechanisms shaping individual preferences of reference frame use and navigation performance. We examine both, nature and nurture-based factors, specifically, gender, age, and cultural backgrounds, and some of their interactions to develop a more complete picture of individual differences in spatial performance and reference frame proclivities.

Gender Differences in Spatial Cognition

Over the last decades, some studies have shown that males outperform females in specific spatial tasks (Moffat et al., 1998; Newhouse et al., 2007). Among the most prominent task examples are the Morris Water Maze (Woolley et al., 2010) and the Mental Rotation task (Masters & Sanders, 1993). In both tasks, males make fewer errors and take less time to solve the task. Furthermore, several studies reported that females are less likely to use an allocentric navigation strategy (Dabbs et al., 1998; Lawton, 1996; Sandstrom et al., 1998). In an attempt to explain the origin of a potential male superior performance in spatial navigation, Perdue and colleagues (Perdue, Snyder, Zhihe, Marr, & Maple, 2011) reviewed several studies to conclude that the range-size hypothesis fits best with the observed data in carnivores. This hypothesis claims that males need to travel larger distances to mate with more females. Roof and colleagues (Roof & Havens, 1992) investigated the biological basis of sex differences in spatial navigation and demonstrated that the “male-hormone” testosterone improves spatial navigation performance in females (Burkitt, Widman, & Saucier, 2007). The above cited studies emphasize the role of biological differences to account for the observed sex differences in spatial navigation. In contrast to such an approach, Saucier and colleagues suggested that differences between men and women simply reflect differences in the underlying navigational strategy (Saucier et al., 2002). In line with such an explanation, Grön and colleagues described differences in cortical areas activated in men and women during navigation, pointing to different navigation strategies (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000). Finally, Hoffmann and colleagues concluded that differences in navigation performance or strategy use between males and females are not based on genetic differences but rather on differences in social hierarchies and educational standards (Hoffman et al., 2011). Generally, the degree and characteristics of gender and social influences on spatial cognition and navigation are still under debate.

Developmental and Aging Aspects of Navigation

The effects of maturation and aging on navigation have gained attention by many researches in the field. The development of brain structures central for spatial cognitive processes (i.e. the hippocampus) already start prenatally and, compared to other regions of the brain, seems to happen rather early (Purpura, 1975). During childhood, several milestones like crawling, upright walking, and the ability to perform head movements are crucially important for the maturation of neural structures, which are in turn important for the development of spatial strategies (Goldman-Rakic, 1987). Besides those early developmental aspects of navigation, lifespan developments have a strong impact on navigation. Most studies found strong evidence of a decline in spatial navigation performance with increasing age (Lord & Marsh, 1975; Moffat et al., 2001; Perlmutter, Metzger, Nezworski, & Miller, 1981; Salthouse, Mitchell, Skovronek, & Babcock, 1989). Moffat and colleagues showed that performance deficits in elderly participants correlated with decreased activation in hippocampal and parahippocampal areas during virtual navigation (Moffat, Elkins, & Resnick, 2006). Holdstock and colleagues performed navigation tasks with patients that suffered from selective hippocampal damage and demonstrated that the loss of hippocampal tissue was associated with the inability to successfully employ allocentric navigation strategies (Holdstock et al., 2000). Similarly, Iaria and colleagues investigated how aging affected the use of particular navigation strategies and corresponding performance. Their results suggest that elderly participants have more difficulties in using allocentric navigation strategies compared to younger participants (Iaria et al., 2009). In summary, most researchers agree that navigation performance decreases with age and that distinct brain regions are important for the use of egocentric and allocentric strategies(Maguire et al., 1998; Moffat, 2009). However the exact relations of changes in neural networks with performance decline in spatial tasks are still widely discussed.

Cultural Influences on Navigation

Over the last decades, cross-cultural research has revealed astonishing differences that have had strong implications in the field of sociology and psychology. One of the most investigated factors was the distinction between individualism vs. collectivism. Markus and Kitayama showed that people from Asian and Western cultures have "*different construal's of one self, of others and the interaction of the two*" (Markus & Kitayama, 1991). They demonstrated that Asian cultures tend to see themselves and others as more interconnected than people in Western cultures and that people from Asian countries try more to fit into a society, while people from Western cultures aim to emphasize their uniqueness and independence. Masuda and Nisbett compared reports about scene perception between Eastern and Western cultures and showed that Eastern people talked more about global scene information, the background, and the environment, while Westerners reported more about single salient objects in a scene (Masuda & Nisbett, 2001). Similarly, Chua and colleagues demonstrated that such different verbal reports were accompanied by different viewing behaviors; American participants fixated longer on the center of the screen while the Chinese participants made more saccades towards the background (Chua et al., 2005). Majid and colleagues showed that the way participants expressed spatial relations varies between cultures (Majid, Bowerman, Kita, Haun, & Levinson, 2004). Haun and colleagues took this idea a step further and demonstrated a correlation between the dominant linguistic spatial reference frame and the dominant reference frame applied in a spatial memory task (Haun et al., 2011). Lovett and Forbus applied a different approach by using a Structure Mapping Engine to model observed differences in spatial problem solving performances between North Americans and the Munduruku, an indigenous South American tribe (Lovett & Forbus, 2011). In summary, investigations on the cultural background demonstrate an impact of culture on many aspects of human behavior and cognition.

Current Study

As described above, there are several factors that influence navigation and spatial cognition in general. Here we investigated how well the factors gender, age, and cultural background can account for individual differences in navigation performance and spatial reference frame proclivity. Specifically, we tested these different factors as predictors. Previous studies have focused on studying these factors mostly in isolation, sometimes by a combination of two factors. To our knowledge, there are very few studies that provide results about all three factors regarding spatial cognition. As a task, we applied a VR star-field path integration task including horizontal (yaw) and vertical (pitch) rotation changes. This paradigm is based on the tunnel task that reliably demonstrated individual differences in reference frame proclivities in virtual navigation with turns in the yaw axis only (Gramann et al., 2005, 2006). While all participants perceive the same visual information in the tunnel task (Gramann, Sharkawy, & Deubel, 2009), different cortical activation patterns were observed for participants using an allocentric or an egocentric reference frame during navigation (Chiu et al., 2012; Gramann et al., 2010; Plank et al., 2010). This paradigm was adapted to spatial navigation in 3D environments, replicating previous results (Gramann et al., 2012). Establishing an online version of the 3D spatial reference frame proclivity task, Goeke and colleagues showed that 207 out of 260 participants could be assigned to either the Turner group, preferring an egocentric reference frame, or the Nonturner group, preferring an allocentric reference frame for navigation (Goeke et al., 2013). Using the same paradigm as Goeke and colleagues, we collected additional data and analyzed reference frame proclivities and performance data from 1823 participants worldwide. For performance analysis we employed two measures, median reaction time and the amount of incorrect responses for each participant. Most importantly, spatial reference frame proclivity was assessed by analyzing the behavioral responses. Altogether this study aimed to reveal the effects and interdependencies of the most important factors regarding spatial cognition within the general population.

3.3 Results

Reaction Time

After an initial cleaning and screening for individuals' spatial reference frame proclivity (see Methods) we first analyzed participants' performance with respect to the independent factors gender, age, and cultural background. Rank transformed and normalized reaction times revealed clear differences for both factors, gender and age (Fig. 1B). Smaller variations were observed for different cultures (Fig. 1A). Accordingly, a three way ANOVA demonstrated significant main effects for the factors gender ($F(1,1147) = 5.17$, $p = .023$, partial $\eta^2 = .005$) and age ($F(2,1103) = 9.00$, $p < .001$, partial $\eta^2 = .016$), and a borderline effect for the factor culture ($F(3,1103) = 2.59$, $p = .052$, $\eta^2 = .007$). None of the two interaction terms considered reached significance. The partial eta squared indicated that age had the strongest impact on the observed variations. Surprisingly, gender had a significant, but weaker influence. Post hoc pairwise comparisons showed that males reacted significantly faster than females ($p < .05$) and that young participants had significantly shorter reaction times compared to middle-aged ($p < .01$) and elderly participants ($p < .01$). Elderly participants had the slowest reaction times but the difference between these participants and middle-aged participants was not significant ($p > .1$). Although overall culture had only a borderline effect, post hoc pairwise comparisons revealed that European participants reacted faster than participants in all other cultural groups North Americans ($p < .01$), Latin Americans ($p < .01$), and Asians ($p < .01$). North Americans reacted slowest, but differences to other cultural groups were not significant.

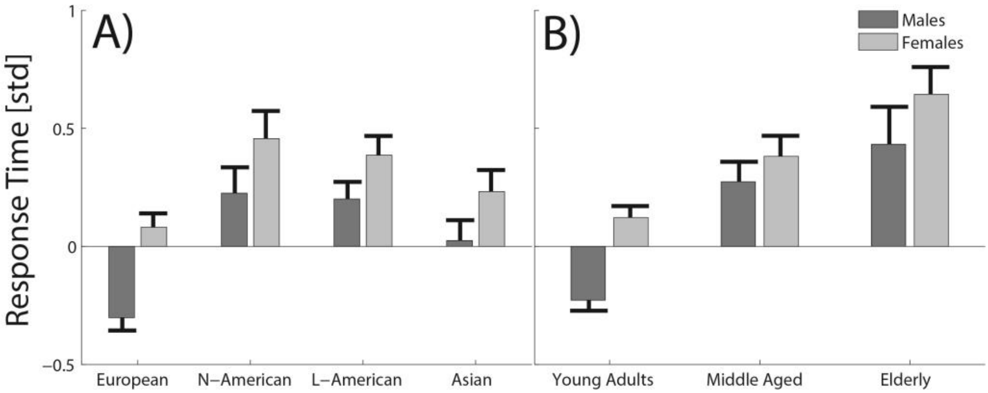

Figure 1: Reaction times for the different subgroup populations. The y-axis shows the mean reaction time in normalized standard deviations. The x-axis separates the different subgroups. Panel **A** shows the reaction times for the different cultural groups, subdivided into males (dark grey bars) and females (light grey bars). Panel **B** shows the reaction times for the three different age groups again separated by the gender factor. The error bars illustrate the standard error of the mean.

Error Rate

Analysis of error rates showed a significant influence of the factor gender (Wald χ^2 (1) = 12.239, $p < .001$) as well as of the factor culture (Wald χ^2 (3) = 27.051, $p < .001$). Figure 2 shows that the proportion of subjects who made at least one error was significantly higher for the female population (light grey bars) compared to males (dark grey bars). Panel A of Fig. 2 reveals that Asians were significantly more likely to make errors compared to the European reference group (Wald χ^2 (1) = 23.682, $p < .001$). Contrasts from other cultural groups did not reach significance. Interestingly, the proportion of subjects who made one or more errors did roughly stay constant with age (Fig. 2B), such that no significant age effect was observed (Wald χ^2 (1) = 1.426, $p = .232$).

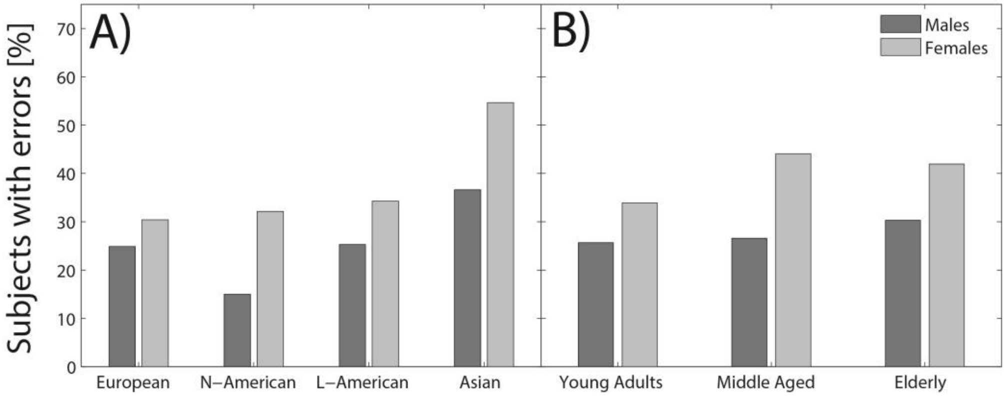

Figure 2: Error rate in the subgroup population. The y-axis indicates the percentage of participants who made at least one (or more) error(s) during the experiment. The x-axis divides the participants into different subgroups. Panel **A** shows the error rates for the four cultural groups, separately for males (dark grey bars) and females (light grey bars). Panel **B** depicts the error rate for the three age groups, again separately for males and females

Spatial Reference Frame Proclivity

To investigate the impact of gender, age, and cultural background on reference frame proclivity, we analyzed the type of reference frame (egocentric vs. allocentric) preferred by participants in the navigation task. Only the factor culture revealed a significant effect (Wald χ^2 (3) = 54.874, $p < .001$). Figure 3A illustrates the ratio of Nonturner (allocentric) participants for the four different cultural groups, separately for both genders. The most prominent difference can be observed between North American and Latin American populations. While North Americans strongly preferred an allocentric reference frame, Latin Americans clearly preferred an egocentric reference frame. Accordingly, the regression results demonstrated that North-Americans more often used an allocentric reference frame than Europeans (Waldχ^2 (1) = 7.106, $p = .008$) while Latin Americans significantly less often used an allocentric reference frame compared to Europeans (Wald χ^2 (1) = 41.416, $p < .001$). Asians did not differ from the European group (Wald χ^2(1) = 0.467, $p = .495$). The factor of gender did not reach significance (Wald χ^2 (1) = 2.477, $p = 0.116$), but the interaction of culture and gender became borderline significant (Wald χ^2 (3) = 7.456, $p = .059$). A closer look revealed a significant gender-culture based deviation only for the Asian population (Wald χ^2 (1) = 7.284, p = .007). This interaction was driven by the fact that females (Fig. 3A, light grey bars) more often used the allocentric reference frame compared to males (Fig. 3A, dark grey bars) in European, North and Latin American populations. However, this principle was reversed in the Asian population; Asian males were more often Nonturner than Asian females. Fig. 3 B shows the differences in spatial reference frame proclivity in the three age groups. Although a small trend towards an egocentric preference in elderly subjects was observed, the factor age (Wald χ^2 (2) = 2.714, p = .099) did not have a significant influence on reference frame use.

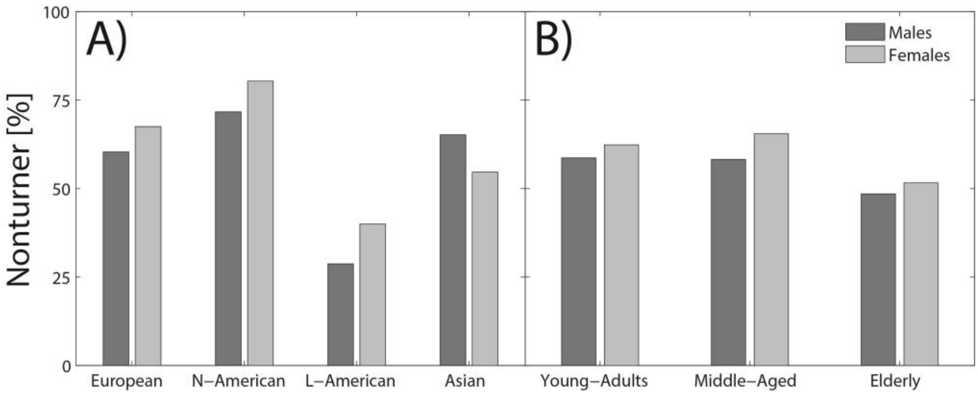

Figure 3: Reference frame proclivities of the subgroup populations. The y-axis shows the percent of Nonturners (compared to Turner) for a given subgroup. The x-axis separates the subgroups by their cultural background (Panel **A**) and age (Panel **B**). The data is again subdivided between males (dark grey bars) and females (light grey bars). The height of the bars illustrates the relative amount of Nonturners in the respective subgroup.

3.4 Discussion

We employed a virtual path integration paradigm with which we recorded data from 1823 participants over the course of about two and a half years. In comparison, only very few studies in the field of spatial navigation have attempted to develop a task that targets such a large overall population, but typically only recruited between ten and fifty participants. A larger database allows for investigation of multiple dependencies and underlines the ecological validity of our results. With this approach we could analyze the influence of gender, age, cultural background and some of their interactions on navigation performance and reference frame proclivity. To our knowledge the current study is the first to provide results with respect to all three factors individually and some of their interactions. Our results demonstrate that gender, age as well as cultural background play, to varying degrees, a role in individual reference frame proclivities.

Overall, the question remains to what extent the reported findings can be generalized and to what degree our results match with other studies investigating navigation. The reference frame proclivity test at hand provides a quite specific and in some way minimalistic approach to studying individual differences in spatial cognition. However, similar to our design, many studies of spatial navigation use virtual environments that only provide visual flow as specific input to derive changes in position and orientation. Here the natural change of idiothetic input during navigation is absent, which might lead to changes in orientation behavior. This was demonstrated by Klatzky and colleagues (Klatzky, Loomis, Beall, Chance, & Golledge, 1998) as well as Chance and colleagues (Chance, Gaunet, Beall, & Loomis, 1998), clearly showing decreased homing performance after path integration with decreasing idiothetic information. Hence, one could speculate that the observed differences in reference frame proclivity might only have been evoked because of the inherent sensory mismatch between visual and proprioceptive information in our study. Indeed, Ehinger and colleagues (Ehinger et al., 2014) demonstrated differential cortical activation in an active, with vestibular and proprioceptive stimulation, vs. passive triangle completion task. Furthermore, earlier studies (Gramann et al., 2010) investigating the tunnel paradigm reveled differential activations of cortical and subcortical structures for egocentric and allocentric reference frame use, indicating different navigational networks to be used by different strategy groups. In addition, Gramann and colleagues demonstrated increases in frontal theta during more difficult aspects of virtual path integration tasks (Chiu et al., 2012; Gramann et al., 2010; Plank et al., 2010). This is in line with results from other virtual navigation tasks like the one used by Kahana and colleagues who implemented a more complex virtual navigation setup and recorded oscillatory subdural activity on epilepsy patients (Kahana et al., 1999). Interestingly, they found an increase in spectral theta power during recall of spatial information. Similarly Bischof & Boulanger reported a correlation of theta band power and task difficulty during maze navigation (Bischof & Boulanger, 2003). Altogether these results indicate that insights gained on the basis of virtual navigation paradigms reflect meaningful and highly relevant features in spatial cognitive processes.

As indicated by both ANOVA results and corresponding effect-size analysis the factor age had the strongest influence on reaction times. This is in line with Moffat and colleagues (Moffat et al., 2001) who found that elderly participants reacted slowest during a navigation task compared to younger participants. However, opposite to earlier findings, we observed an approximately constant error rate across different ages. A possible explanation for this is that the age range of elderly participant included subjects 50 years of age and older, with an average age of about 60 years with heterogeneous subgroups. Indeed, many other studies have tested elderly participants that were ten to twenty years older than participants in the present study. Thus, a direct comparison of the present results with other studies on age-related changes in navigation should be treated with care, and a larger sample of older participants aging 70 and older might potentially show a stronger age effect. Furthermore, it is noteworthy to mention that erroneous responses might have happened due to a variety of reasons. Individual high error rates lead to the assumption that a particular subject has rather poor spatial cognitive abilities. However some participants might have had troubles understanding the task demands, a flawed visual perception and/or a wrong interpretation of the arrows' pointing direction. All these factors could also have led to an increase of error rate. Finally very few (<1%) subjects had extremely high error rates, which might have been present due to distraction or lack of attention during the task.

As expected, the factor gender significantly influenced both reaction times and error rates. Males responded faster and made fewer errors than females. Such a male advantage is in line with several previous studies (Masters & Sanders, 1993; Moffat et al., 1998; Newhouse et al., 2007; Woolley et al., 2010). Interestingly, this male advantage was present throughout all cultures and age groups for both types of performance measures. The absence of performance-based interaction effects suggests that the observed male advantage in this spatial navigation task is a rather general phenomenon and not limited to a certain culture or age group. One reason for the male superiority in spatial performance might be more training, in particular with virtual (computer based) navigation. Several studies have shown that playing computer games improves mental rotation skills 53 and pointing accuracy

(Cherney, 2008; Lawton, 1994). Furthermore, social expectancy and task anxiety might have had a strong impact of the observed gender differences. Moè & Pazzagli (Moè & Pazzaglia, 2006) found that women have a lower expectancy in spatial task performance and that this lowered confidence, causing worse performance during navigation (Cooke-Simpson & Voyer, 2007; Maryjane Wraga, Duncan, Jacobs, Helt, & Church, 2006). Lawton and colleagues (Lawton, 1994) showed that women demonstrate higher anxiety levels during such tasks, which also reduced task performance (Schmitz, 1997). In summary, several factors contribute to the overall lower spatial performance observed in the female group. However, the additional influence of cultural background on navigation performance is compelling. In particular, European participants reacted quicker than anyone else and Asian participants made significantly more errors than other cultural groups. However, more detailed investigation regarding socio-economic influences must be carried out to understand the underlying mechanisms of such effects. In essence, the results of our performance measures are compatible with the literature in the field and extend and attribute an influence of all three factors on performance measures.

Unexpectedly, the analysis of spatial reference frame proclivity revealed a significant effect of cultural background only, while there was no main effect of the factors gender or age. Particularly surprising is that gender factored in only by an interaction with cultural background. The majority of earlier studies reported that females preferred egocentric strategies over allocentric strategies(Dabbs et al., 1998; Lawton, 1996; Perdue et al., 2011; Sandstrom et al., 1998). Our results argue against such conclusions and suggest that gender differences in spatial reference frame proclivity are dependent on the cultural background of participants. In particular, our findings suggest that Asian males use an allocentric reference frame more often than Asian females, while for European, North and Latin American populations such a gender effect is reversed. The hypothetical decline of an allocentric navigation reference frame with increasing age was only slightly visible in our data. However, sampling in the elderly groups was rather poor and heterogenic. In the future, a denser sampling for elderly participants will be pursued to investigate this question. Most surprising was the particularly strong influence of cultural background on spatial reference frame proclivity. Here, it is worth mentioning that the definition of egocentric and allocentric reference frames as we used them in our study, also correspond to the definition of reference frames in a linguistic sense. Levinson’s abstraction of spatial frames of reference (FoR) describes three different forms of reference frames (Levinson, 1996; Levinson, Kita, Haun, & Rasch, 2002; Majid et al., 2004). The 'Relative FoR' uses a coordinate system that is aligned with the cognizing subject and can be roughly compared to an egocentric reference frame used in our study. The second FoR describes the 'Absolute FoR' that uses fixed bearings like magnetic north, which is again highly similar to the definition or our allocentric reference frame. The last FoR according to Levinson is the 'Intrinsic FoR' that provides coordinates centered within an object that provides canonical orientation (e.g., a car with a defined front and rear end). However, for large-scale spatial tasks with no unique other objects involved the intrinsic FoR might be not as useful as compared to small scale tasks (e.g. table-top arrangements) because objects might be too large or far away to be clearly recognized or to provide useful object orientation information. In general, an allocentric reference frame was used more frequently in all cultures except the Latin American culture. However, strategies did not vary along the dimensions commonly discussed in cross-cultural psychology, i.e., Western vs. Eastern populations (Chua et al., 2005; Markus & Kitayama, 1991; Masuda & Nisbett, 2001). This supports the idea that culturally related preferences in spatial reference frame proclivities are generated by other mechanisms than those investigated by most cross-cultural studies. In particular, the concept of collectivism vs. individualism seems to not be an adequate model for explaining the observed effects. However, both North and Latin American cultures significantly differed from the European reference group. The fact that these findings are equally present in both males and females supports the validity of the observed effect. Nevertheless, the characteristics of the observed differences are not fully understood. Why do Latin Americans overall prefer an egocentric and North Americans an allocentric reference frame? Brown and Levinson (Brown & Levinson, 1993) investigated the spatial language use of the Mayan language Tzeltal. They reported that both groups avoid egocentric terms in their language compared to English speaking people. Similarly, Levinson (Levinson, 1997) showed that the Guugu Yimithirr, an Australian aboriginal tribe, describe spatial relations using absolute or allocentric reference systems compared to people from Western languages who use egocentric coordinates (left, right). On the first, view it might be tempting to relate the Latin American population in our study to the indigenous populations of Brown and Levinson; however, the direction of the observed effect is reversed. Moreover, in contrast to those indigenous people the vast majority of participants in our study, including the ones from Latin America were urbanized and in one way or another related to a university context. Hence the daily navigation scenery of both the Latin and the North American group was rather comparable. An alternative interpretation is related to the socio-economic factors that vary across different culture groups. As Hoffman and colleagues reported, variations in educational standards and social hierarchies could account for observed differences in spatial performance between males and females (Hoffman et al., 2011). In fact, several underlying socio-economic variables might have generated such culture effects and future studies need to investigate this in more detail.

3.5 Methods

Online Navigation Task

For the purpose of present study, we translated the web page (http://www.navigationexperiments.com/TurningStudy.html) into 10 different languages (German, English, French, Spanish, Portuguese, Russian, Turkish, Chinese, Thai, and Korean) and established cooperation between different research groups, which all advertised the study locally and recruited participants with varying ages and genders. A back translation validated that the instructions and questionnaire were correctly translated between the different languages. Overall, we followed two approaches during data collection. Most importantly, we aimed to obtain a high number of participants for each age, gender and cultural subgroup, in order to allow proper statistics. Second, we targeted the general audience and tried to reach as many subjects as possible. All of the participants performed the experiment independently with detailed instructions given during the procedure. All of the subjects were informed about the purpose of the study, and informed consent was obtained from all of the subjects during the procedure. Data recording was carried out in accordance with the approved ethics guidelines of the University of Osnabrück. The experimental protocols were approved by the Ethics Committee of the University of Osnabrück.

As a navigation task, we used the tunnel paradigm, originally proposed by Gramann and colleagues, as it provides a fast and clear categorization of the preferred spatial reference frame (Gramann et al., 2005). The task of the participants in this particular paradigm was to choose one out of 4 homing arrows

(Fig. 4B) that indicates the way back to the starting position (homing arrow) after a visually presented path (Fig. 4A). Each path was constructed such that an initial straight segment was followed by a turning segment (left, right, up or down). Three different turns were used with 30, 60, and 90 degrees. After every stimulus turn was another straight segment. All of the segments were visible for about three seconds and smoothly transitioned into one another. The combination of each direction (4) and angle (3) was rendered as a separate video in "mp4" format and displayed using Flow Player®. Each video was shown twice in a randomized order, such that all of the participants performed 24 trials. Questionnaire data were retrieved after the tunnel task. The participants could use either an egocentric (Turner) or an allocentric (Nonturner) reference frame (see Fig. 4C), associated with distinct homing arrows. The essential difference between both strategies is based on whether the participants updated their cognitive heading along with the stimulus turn seen on the screen. In the lower panels of Fig. 4C the human navigator changes (updates) her cognitive heading direction according to the heading changes indicated through changes in visual flow. As a consequence, she chooses an arrow pointing "up and back" after passage with a turn upwards and "right and back" after a passage with a turn to the right. Reversely, the other two drawings show a human navigator who does not update her heading according to visual flow changes during the stimulus turn. Therefore, the navigator points "down and back" after a passage with a turn upwards and "left and back" after a passage with a turn to the right. From here on, we call the first type of reference frame users "Turner" or egocentric and the second type of reference frame users "Nonturner" or allocentric. There were two additional arrows pointing into wrong directions (i.e., to the left or right after a passage up or down, or up and down after a passage to the left or the right) serving as catch responses (erroneous responses).

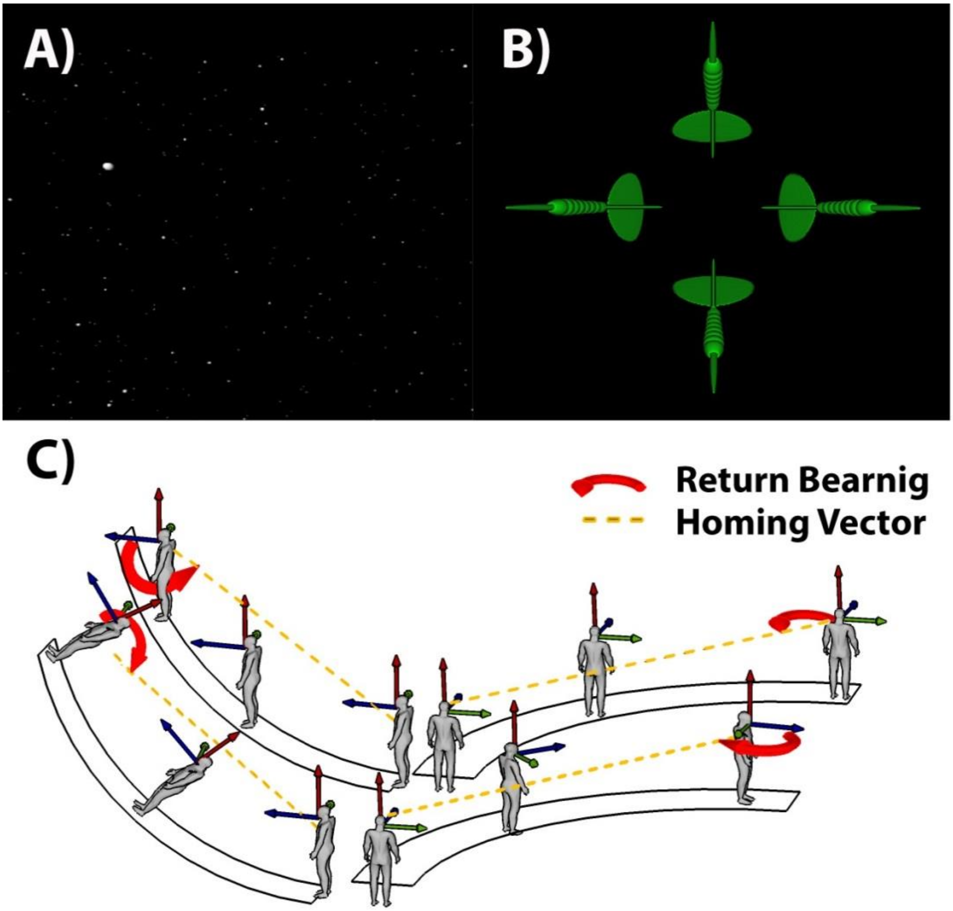

Figure 4: Experimental paradigm. A) Screenshot of the star-field passage in the online navigation experiment. During the passage, the white dots (stars) induced visual flow, indicating a turn into one direction. **B**) Forced choice arrow selection in the experiment after a 60-degree, rightward turn. The arrow pointing to the right indicates the homing vector in line with an egocentric reference frame; the arrow pointing to the left is congruent with an underlying allocentric reference frame. Choosing one of the other two arrows (up and down in this case) was counted as an incorrect response. **C**) Turner and Nonturner responses, respectively in a schematic 3D drawing. The two upper drawings display the spatial reference frame proclivity for a Nonturner (allocentric) navigator during the turning segment. Most importantly, Nonturners do not change (update) their cognitive heading during the turning segment. The upper-left drawing shows the Nonturner spatial reference frame proclivity on a pitch trial, while the upper-right drawing shows a yaw trial. The yellow path indicates the homing vector back to the starting location. The red, curved arrow displays the return bearing at the end of the turning segment. The two lower drawings show a Turner (egocentric) navigator during pitch (left) and yaw

(right) navigation. Importantly, the Turner updates his/her cognitive heading during the turning segment and therefore has a return bearing (red arrow) that is mirror-reversed compared to the Nonturner's bearing.

Participants

Over the course of 34 month, 1823 participants performed the online experiment. We excluded all participants with incomplete or ambiguous (e.g. naming no or more than one country for cultural background) data, teenagers below the age of 18, and people from those geographic regions with sparse sampling (see Cleaning & Clustering section). Consequently, 372 participants were removed from the dataset and the remaining 1451 participants were used for analysis. Out of these, 872 (60.10%) were males and 579 (39.90%) were females. The grand average age of the participants was 26.23 years (SD = 11.47). Overall, we were able to recruit participants from over 30 countries and 4 continents. Although the participant distribution was not equal across all of those countries, each of our cooperation partners in Spain, Thailand, Mexico, and the U.S. recruited at least 150 participants. As the study was advertised by various research institutes in an academic context, most participants were related to a university context. In total, 205 of all 1451 participants were left handed. No participant received reimbursement for the experiment, but all of the participants were offered information on their preferred reference frame at the end of the experiment.

Determining Reference Frame Proclivities

The spatial reference frame proclivity categorization was performed in accordance to previous studies. In short, we categorized all subjects according to their ratio of allocentric and egocentric responses (not taking erroneous responses into account) into one out of five classes (Turner, Nonturner, Switcher, Inverse Switcher and No Preference). Figure 5 illustrates this classification. The Participants who used the allocentric response in at least 75% of all cases were classified as Nonturners (upper-right corner), while the participants using the egocentric reference frame in at least 75% of cases were classified as Turners (lower-left corner). Switchers and Inverse Switchers changed reference frame use depending on the axis of rotation, while the "No Preference" participants randomly switched between the reference frames. For more information about the category labeling, category boundaries and parameters used, see and Goeke and colleagues (C. M. Goeke et al., 2013).

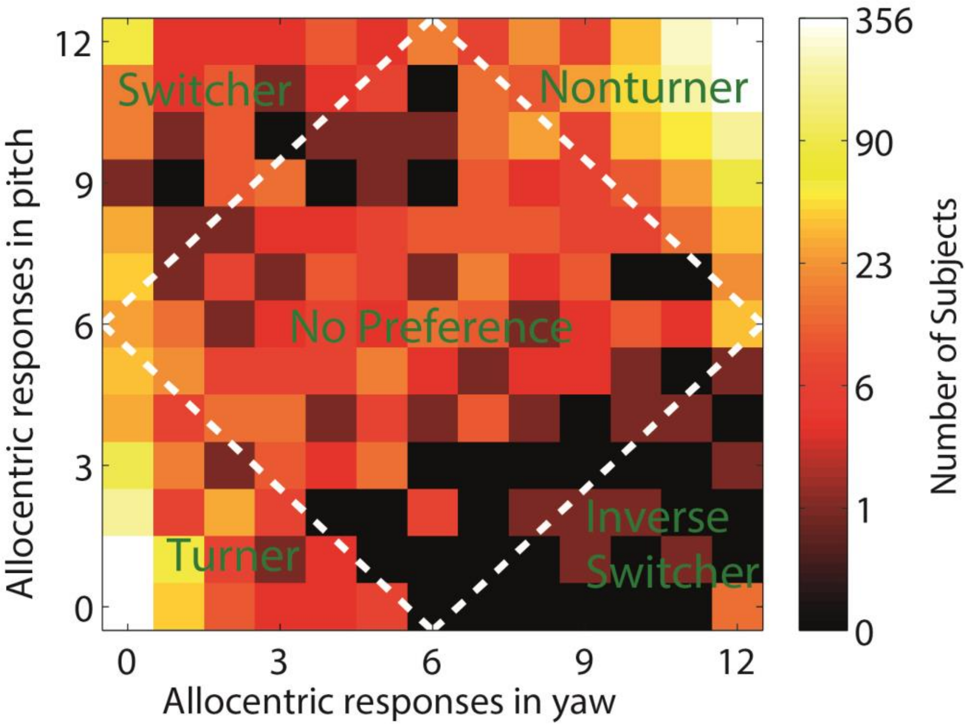

Figure 5: Classification of all subjects into reference frame strategy groups. The y-axis indicates the number of allocentric responses in pitch, the x-axes indicates the number of allocentric responses in yaw. The color of the squares reflects the number of subjects with identical ratios of allocentric vs. egocentric responses for both yaw and pitch (bright yellow indicates many subjects; dark brown indicate few subjects). The logarithmic scale to the right shows the number of subjects corresponding to each color, with rounded values. The white, dashed line marks the boundaries between the reference frame strategy groups. Additionally, the labels (in green) indicate the names of the respective strategy groups.

Cleaning & Clustering

We needed to ensure that the sample size of each investigated subgroup was large enough to be able to perform valid statistical tests. Two restrictions had to be made due to this statistical consideration. First, we could not investigate all of the interactions among our independent factors. Second, the participants who were too young, came from a geographic region with very few participants, or did not have a clear proclivity for a spatial reference frame (Turner or Nonturner) were excluded from the data set. Specifically, we were only able to recruit 5 participants from Latin America aged 50 years or older. As a consequence, we decided to not include the 2-way-interaction of culture and age or the 3-way interaction of culture, age and gender. Instead, for all of the subsequent analyses, we only considered the main effects of age, gender, and culture; the 2-way interaction of gender and culture; and the 2-way interaction of gender and age.

The gender analysis was simplest using the dichotomous response from the participants. Cultural categorization was based on the question: “In which country did you grow up”. However, again considering the sample sizes, we were not able to analyze each country individually. Hence, we decided to group all of the countries with respect to geographical closeness, which is one of the most intuitive ways to coarsely separate different cultures. As a result, we assigned all participants to one out of four cultural groups (Europe, North America, Latin America and Asia). The remaining participants with cultural backgrounds other than those mentioned above were removed from the data set because their total sample sizes were too small for further statistical analysis. Regarding age, we first excluded all of the participants who were younger than 18, as we could not ensure that those participants had performed the study independently by themselves. Then, we divided the participants into one out of three age-groups: young adult, middle-aged and elderly participants (young-adult: range = 18–30 years, mean = 21.54 years, SD = 3.52 years; middle-aged: range = 31-50 years, mean = 37.05 years, SD = 5.69 years; elderly: range >50 years, mean = 60.53 years, SD = 10.54 years).

Finally, we also needed to ensure a rather homogenous distribution of our categorical dependent variable, namely spatial reference frame proclivity. Overall, the subjects were assigned to one out of five possible strategy classes. However, the group sizes of participants other than Turner or Nonturner were relatively small and could not be statistically analyzed after in combining our independent factors (e.g. young female Switchers from Asia), again due to too small sample sizes. Consequently, the data analyses focused only on the distribution of the two main reference frame strategy groups; hence we removed the participants who followed a different minor strategy. In total we removed 372 subjects from the data set, leaving 1148 subjects for the consequent analyses of spatial reference frame proclivity and performance. As a result, each investigated subgroup (see Table 1 and Table 2) had at least 30 participants, which ensured valid statistics.

Subgroup / Strategy	Males				Females				Σ
	European	N-American	L-American	Asian	Euro-pean	N-American	L-American	Asian	
Nonturner & Nonturner	426 29.36%	60 4.14%	87 6.00%	112 7.72%	240 16.54%	56 3.86%	70 4.82%	97 6.69%	1148 79.12%
Other Strategies	110 7.58%	16 1.10%	18 1.24%	43 2.96%	67 4.62%	4 0.28%	8 0.55%	37 2.55%	303 20.88%
Σ	536 36.94%	76 5.10%	105 7.24%	155 10.68%	307 21.16%	60 4.14%	78 5.38%	134 9.24%	1451 100%

Table 1: Gender-cultural participant distribution. The table shows the total number and fraction of Turner plus Nonturner participants (second row), compared to subjects using a minor reference frame strategy (third row). The last row illustrates the sum of all reference frame strategy groups. Columns two to nine separate the subjects according to their gender and cultural background. The four left columns show the number of male subjects having a European (2), North-American (3), Latin-American (4) and Asian (5) cultural backgrounds, while the four right columns are for female subjects, respectively. The last column sums up the culture and gender groups.

Subgroup / Strategy	Males			Females			∑
	Young Adults	Middle-Aged	Elderly	Young Adults	Middle-Aged	Elderly	
Nonturner & Nonturner	573 39.49%	79 5.44%	33 2.27%	348 23.98%	84 5.79%	31 2.14%	1148 79.12%
Other Strategies	155 10.68%	16 1.10%	16 1.10%	78 5.38%	24 1.65%	14 0.96%	303 20.88%
∑	728 50.17%	95 6.55%	49 3.38%	426 29.36%	108 7.44%	45 3.10%	1451 100%

Table 2: Gender-age participant distribution. The table shows the total number and fraction of Turner plus Nonturner participants (second row) compared to the subjects using a minor reference frame strategy (third row). The last row illustrates the sum of all reference frame strategy groups. Columns two to seven separate the subjects according to their gender and age. The three left columns indicate the number of young males (2), middle-aged males (3) and elderly males (4). The three right columns show the same for young females (5), middle-aged females (6) and elderly females (7), respectively. The last column sums up the gender and age groups.

Analysis

For the analysis of reaction time, we first calculated the median response latency for each participant. The resulting distribution of response times over subjects was not normally distributed; rather it was slightly skewed in the positive direction meaning that most of the participants reacted rather quickly and only a few participants reacted slowly (Fig. 6A). Hence, in a second step we rank transformed reaction time data and mapped the resulting values to a Gauss distribution with mean 0 and standard deviation 1 to reach a normal distribution (Fig. 6B). Having fulfilled the normality requirement, we employed an ANOVA with reaction time as a dependent variable and age, gender and cultural background as fixed effects and independent factors. Finally, we used Turkey's honest significant difference (HSD) test to compare the individual differences between the various subgroups.

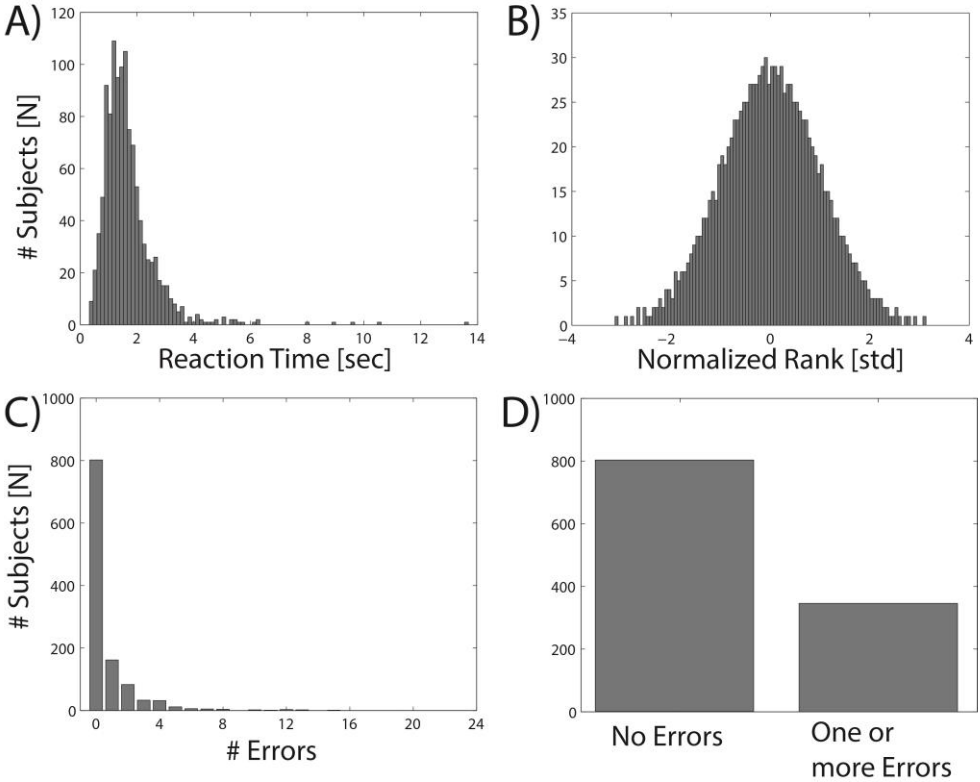

Figure 6: Distribution properties of the performance measures. Panel **A** shows the distribution of median reaction times for all of the participants. Panel **B** illustrates the distribution of reaction times after a normalized rank transformation. Panel **C** shows the histogram of errors for all of the participants. Panel **D** illustrates the distribution of participants into the two error groups (no errors, one or more errors.

The second measure of navigation performance was defined as the amount of incorrect responses by each participant. We counted an error if a participant chose an arrow pointing horizontally after a vertical passage or vice versa, as such a behavior indicates a confusion of the yaw and pitch axes. However, most of the participants did not make any errors (Fig. 6C). Hence, calculating the average number of errors suffered immensely from outliers (subjects with 5 or more errors) and thus violated the homogeneity of variance assumption necessary to perform a parametric test. In order to still test for differences regarding error rate, we transformed the data into a binary variable: participants with one or more errors vs. participants without errors (Fig. 6D). After this transformation, we employed a binary logistic regression with gender and culture as categorical predictors, age as an ordinal predictor, and "error-group" (0 or 1) as the binary response variable. We used a stepwise approach (Wald forward) to find the model that best fitted the data. As a reference category, we chose the most common groups for each investigated factor (Males, Young Adults and European) in order to avoid false discoveries due to data sparseness.

The focus of the reference frame investigation was based on the two dominating reference frame strategies in the current paradigm (Turner vs. Nonturner). There were 686 Nonturner and 462 Turner in our filtered sample data, resulting in a baseline ratio of 59.76% Nonturners. We hypothesized that this ratio of Turner vs. Nonturner participants varied significantly between males and females, different age groups, and culture subpopulations in our dataset. As we intended to use the spatial reference frame proclivity as the dependent variable, we decided to perform a binary logistic regression, similarly to the analysis of error rate. Again, gender and cultural background were used as categorical predictors, while age was used as an ordinal predictor. We used the participants' spatial reference frame proclivity (0 = Turner, 1 = Nonturner) as the binary response variable. We used the same reference categories (Males, Young Adults and European) as in the error rate analysis and again applied a stepwise (Wald forward) approach.

Acknowledgements

Most of all, we would like to thank everyone who helped to promote the online navigation study, in particular Prof. Victor Solis-Maciasa and Prof. Sue Becker for their very effective advertisement. Special thanks to Jessica Schwandt, Jose Ossandon, Aleksey Lytochkin and Susan Wache who helped translate the questionnaire into a variety of languages. This work was funded by the European research grant: ERC- 2010-AdG #269716 – MULTISENSE, together with the Cognition and Neuroergonomics/Collaborative Technology Alliance #W911NF-10-2-0022.

4. Study Three: The Alignment Study

This study is currently submitted to “Nature Scientific Reports”

Are non-egocentric spatial reference frames compatible with enacted theories?

Goeke C., König, S. U., Meilinger T., König P. (submitted).

4.1 Abstract

Enactivism theories propose an action-oriented approach to understand human cognition and thereby change the perspective of how we understand the human mind. So far, however, empirical evidence supporting these ideas has been sparse. Here, we test predictions on performance in spatial tasks cast in allocentric reference frames based on an enactivist framework. Overall, two groups of participants performed two object orientation tasks and one pointing task: Our results demonstrate that under time pressure the relative orientation of two houses can be retrieved more correctly than the absolute (cardinal) orientation of single houses. Performing these tasks either without time pressure or with streets as stimuli, revealed the opposite result pattern. Pointing to a house yielded overall the best performance. This suggests that: (i) Orientation information about localized objects such as houses are originally coded in object-to-object relations while cardinal information is deducted via cognitive reasoning, (ii) Orientation information for objects that are directly used for actions (i.e. streets) are preferentially coded in cardinal orientations and relative orientation has to be deduced. This pattern of results supports the view that spatial information about object orientation and location is primarily learned in an action oriented way as proposed by an enactive framework for human cognition.

4.2 Introduction

Theories of embodied cognition understand cognition as being derived from the body’s interactions with the world (Thompson & Varela, 2001; Wilson, 2002).The enactive approach within embodied cognition theories emphasizes the importance of action, stating that even perception is for action (Noë, 2004; O’Regan & Noe, 2001). The more radical accounts of enactivism (S. Gallagher & Varela, 2003; Hutto & Myin, 2013; Thompson, 2007) even reject the classical view of cognition as internal representations of the environment. Instead, these theories assume that cognition is embodied activity that includes the mind, the body and the environment and stress the importance of action (Engel et al., 2013). Hence, approaches of embodied and enacted cognition provide modern frameworks to address current topics in cognitive science (Maye & Engel, 2013)

Can we find empirical evidence for the enactive approach in the area of spatial cognition, a field of research that is naturally centered on interaction within the environment? A central aspect in spatial cognition is the differentiation of human navigation strategies based on two broad classes of reference frames, i.e. egocentric and allocentric reference frames (Burgess, 2006; Gramann, 2013; Klatzky, 1998; Mou, McNamara, Valiquette, & Rump, 2004). Based on the work of Klatzky (Klatzky, 1998) the egocentric reference frame is defined as relating the environment to the observer’s physical position and orientation. Somatosensory information is gathered while moving in the environment and, as the sensors are part of the body and move with the body, initially coded within an egocentric reference frame. Spatial updating then involves changes in egocentrically coded sensory information (Riecke, Cunningham, & Bülthoff, 2007) and is linked to self-motion (Simons & Wang, 1998; Wang & Spelke, 2000). In contrast, allocentric reference frames are defined as being based on cardinal directions, geometric features or environmental cues such as objects rather than the observer’s body (Klatzky, 1998) Thus, spatial cognitive processes based on egocentric reference frames are naturally phrased within the framework of enacted cognition, but it needs further investigation, whether navigation based on allocentric reference frames can also be understood within an action oriented approach.

In recent years, however, a more complex taxonomy of spatial reference frames was introduced by Meilinger and Vosgerau (Meilinger & Vosgerau, 2010) Complementing the classical reference frames they suggested sensorimotor representations and perspective free representations as a second form of egocentric and allocentric spatial representations, respectively. The former type relates directly to the work on sensorimotor contingencies by O'Regan and Noe (O'Regan & Noe, 2001). This theory proposes that perception is constituted by the mastery of sensorimotor relations, i.e. the knowledge how the sensory signals change contingent on the own actions. In the context of navigation, changes of the retinal image relates directly to the movement vector and distance to the agent. For example, in comparison to proximal locations the projected images of distant locations change little when translating a step to the side. Sensorimotor contingencies are directly relating perception and action and, thus, qualify as truly egocentric representations (Engel et al., 2013). Perspective-free representations are a non-centred variation of allocentric reference frames (Meilinger & Vosgerau, 2010). They can be based, for example, on a structural description specifying of pair-wise distances and/or angles. There is no natural centre or origin of a coordinate system. Then, the representation cannot be described by a standard coordinate centred allocentric representation. Furthermore, it appears that an explanation of human behavior based on the set of four elementary spatial representations alone faces severe difficulties. Objects, we interact with, are often hierarchically structured on multiple spatial scales. An example might be shopping in a city, where the most relevant streets and shops have to be located. Then, on another scale, the entrance of a selected shop has to be used, i.e. pressing the door handle. Including all that information in a single representation with one flat hierarchy seems implausible. Object parts, like the mentioned door handle, are an example mixing egocentric and allocentric reference frames. Surely, object parts are naturally coded in relation to the whole object, i.e. an allocentric reference frame. Yet, the objects themselves are encoded from experience views, i.e. an egocentric perspective (O'Regan & Noe, 2001; Simons & Wang, 1998). As a consequence, many theories of spatial learning suggest that knowledge based on different reference frames develops (Haith & Benson, 1998; Nardini, Burgess, Breckenridge, & Atkinson, 2006; Piaget & Inhelder, 1967; Siegel & White, 1975; Wang & Spelke, 2000) and is used in parallel and interact (Burgess, 2006; Gramann, 2013; Hodgson, 2006; Ishikawa & Montello, 2006).

A large body of experimental results supports these theories For example, viewpoint-dependent scene recognition (Diwadkar & McNamara, 1997) or pointing accuracy (Shelton & Mcnamara, 1997) was shown to improve when the tested viewpoint was aligned with the viewpoint from which the scene was learned. Other researchers also found that the performance of participants was improved when imagined self-orientation was aligned to own body orientation (Kelly, Avraamides, & Loomis, 2007) which is an example of an alignment of egocentric aspects. Also an alignment of the observer's viewpoint with an intrinsic axis of an object array (Mou & McNamara, 2002), which represents aspects of the surrounding environment, improved pointing accuracy from imagined viewpoints. Combining egocentric and allocentric aspects Mou and McNamara (Mou & McNamara, 2002) investigated how locations of objects in a new environment are learned and stored in memory and introduced an intrinsic reference frame depicting interobject spatial relations. This intrinsic reference frame specifies object-to-object relations, i.e., it is allocentric. However, its orientation may be adopted from egocentric and environmental cues (Greenauer & Waller, 2008). Remembered allocentric spatial relations guide egocentric action in space, which is updated while moving in the environment (McNamara, 2002). This conclusion is supported by McNamara et al (McNamara, Rump, & Werner, 2003) who showed that participants learned objects' locations in a large-scale natural space by actively walking. Pointing accuracy was improved when viewpoints were either aligned with a salient landmark or with the walls of a central building. Thus, information related to an allocentric reference frame is combined with egocentrically coded information to be translated for spatial action.

In the present study, we investigated, whether spatial knowledge based on non-egocentric reference frames, is nevertheless coded and utilized in an action oriented way. We select stimuli in the form of houses and streets of a single city (see below). The two variations of allocentric reference frames described above differ in their accessibility to action relevant information. The classical allocentric reference frame codes location and orientation of the stimuli separately for each object. An advantage of this strategy is efficiency as the amount of information to be stored scales linearly with the number of objects. In contrast, gaining information for spatial behaviour, e.g. navigating from one location to another, requires access to the information of start and goal location, and additionally cognitive processes combining this information. Thus, when accessing action related information, storage efficacy of this strategy is paid for by a time penalty. Alternatively, in a perspective-free reference frame information of the locations of the stimuli are primarily learned and stored in relation to other stimuli. As a disadvantage, the amount of information to be stored scales supra-linearly (e.g. quadratically when assuming all to all relations) with the number of objects. However, retrieving information for spatial behaviour, e.g. navigating from one location to another or pointing from one location to another location, only requires direct access to the stored relation of starting and goal locations without further cognitive considerations. Thus, this approach yields an advantage in speed at the expense of storage needs. Thus, these two types of coding differ qualitatively in terms of storage needs and speed of access to action relevant information.

To further investigate these two types of coding of spatial information and not naively equate the specific experiments to forms of spatial reference frames we call, for the purpose of the present study, the two types of coding unitary code and binary code, respectively. A *unitary code relates* the information to a single object, whereas a *binary code* relates to a combination of objects. In view of the complementary advantages and disadvantages it is well conceivable that humans may use one or the other of both strategies.

We performed two main experiments to address coding of spatial information for single objects and for object-to-object relations. Both experiments were realized with two different stimuli sets: front on views of houses as localized stimuli and views along streets as the means to navigate from one location to another. Thus, we deliberately ignored navigation within houses or the relation of streets of different cities and limit the stimuli of this study to a single level of spatial information. Furthermore, a pointing task with house stimuli was performed as a reference test. Please note, that here our primary focus lies on allocentric reference frames and not on the influence of bodily alignment relative to the stimuli shown. The influence of bodily position during the experiment is analyzed only as a secondary aspect. To differentiate, whether participants could directly access the required spatial information or whether further cognitive processing steps were needed, participants either performed under time pressure or had unlimited time for responding (for further details see method section). Specifically, we tested the following hypotheses:

- H_0: Spatial information about localized objects such as houses is coded separately for each object relative to a common centre of the reference frame, i.e. orientation of an object in cardinal directions (*unitary code*). Accessing action relevant relations between objects out of the unitary information requires time consuming cognitive reasoning. This hypothesis is compatible with a classical allocentric reference frame for storing spatial information on the location of houses.
- H_1: Spatial information, i.e. orientation, about localized objects such as houses is coded in direct relation to other objects (*binary code*), without the necessity

of a common centre of the reference frame for all objects. This direct coding of object-to-object relations allows for an intuitive and fast access of between-object relations, thus it is suitable for the generation of behaviour. This hypothesis is compatible with a perspective-free allocentric reference frame for storing spatial information on the location of houses.

- H_2: Information relating to stimuli that connect objects such as streets is directly accessible and coded differently than houses (*unitary code*). Thus, in this case the retrieval of directional information directly relevant to an action, e.g. driving in a specific direction on a street, needs no time consuming cognitive processing. This hypothesis is compatible with a classical allocentric reference frame for storing spatial information on streets.

Summarizing, the present study tests the availability of unitary and binary coding of spatial knowledge for human behaviour.

4.3 Results

Testing access information relating to single objects and to object-to-object relations

With two tasks we separately assessed the ability to estimate the orientation of houses in relation to the north cardinal direction (*absolute orientation task*) and the ability to relate to the relative orientation of houses (*relative orientation task*). In the first task we showed real world frontal view photographs of houses in the city of Osnabrück area (Figure 1). On each of 156 trials, we presented two images showing the same photograph above each other on two separate screens to the participants. Each of the two images was overlaid with an ellipsoid, in with an arrow pointed into a particular direction. One of the arrows was pointing into the north cardinal direction. The other arrow was pointing into a direction that differed between 0-330° (in steps of 30°) to the north arrow. The participants had to choose the image where the arrow pointed correctly towards north by pressing either an upward or a downward button on a response box.

Figure 1: **Absolute orientation task.** The illustration shows one example trial of the absolute orientation task using house stimuli. As shown in the figure the same image of a known object was presented twice above each other. Additionally, each image was overlaid with an ellipsoid and an arrow inside that ellipsoid that pointed into one specific direction. One of the arrows was pointing to the true north cardinal direction within the image (in this case the upper image), while the other was pointing in a different direction in steps of 30°. The task of the participants was to select the image (arrow) that pointed correctly towards the north direction.

We designed the second, relative orientation task to be comparable to the absolute task (Figure 2). Hence, as stimulus material, we used the same frontal view photographs of the Osnabrück city area. Each trial of the 72 trials consisted of a fixed triplet of images, one priming image and two target images, which were selected beforehand (see methods). On each trial, first the prime picture was shown on both screens for 5 seconds. After the prime stimulus was turned off, the two target stimuli appeared, one on the upper, the other on the lower screen. The task of the participants was now to select one out of the two target images whose orientation was more closely aligned with the orientation of the prime image. As an example let us consider that the prime stimulus is facing westwards and the first target is facing westwards as well, while the second target is facing north. As a result, the first target would be more similarly oriented to the prime than the second target, which is why the first target image would be the correct choice.

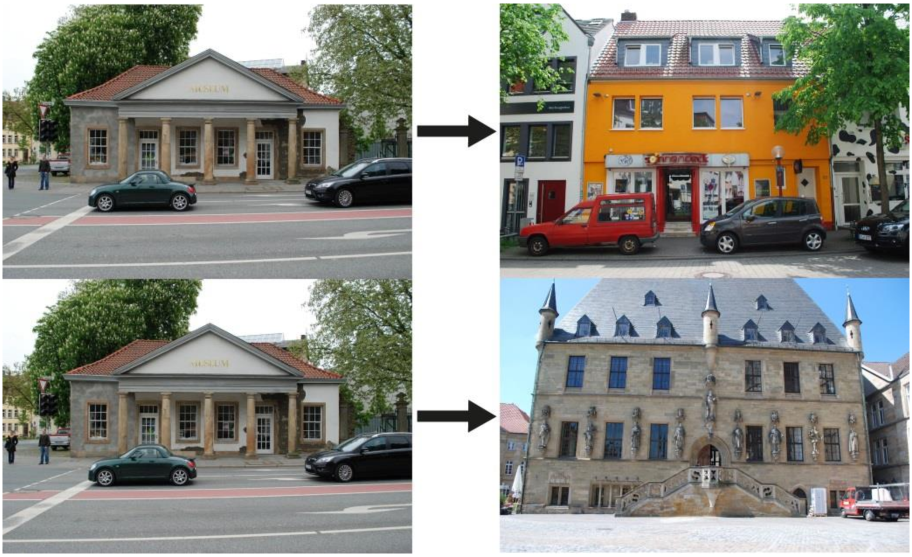

Figure 2: **Relative orientation task.** The illustration shows one example trial of the relative orientation task using house stimuli. First a prime image (left) was shown for five seconds. Then two different target images appeared on the two screens above each other (right). The house in one of the target images (here the upper one) was facing the same direction as the prime, while the house in the other picture was facing towards a different direction in steps of 30°. The task of the participants was to select the image that was facing the same direction as the prime.

Assuming that the participants used a *unitary code* (H_0) it would allow for direct access to the relevant information in the absolute orientation task, but would require separate access to the information of both objects and, some additional cognitive considerations in the relative orientation task. H_0 thus predicts high performance in the absolute orientation task, even at short reaction times, but low performance in the relative orientation task at short reaction times, improving in the absence of time pressure. Given a *binary code* (H_1), in the absolute orientation task the required information is not directly accessible, but necessitates cognitive reasoning, in contrast to the relative orientation task in which the required information is directly accessible, even at short reaction times. Therefore, a *binary code* causes a low performance in the *absolute orientation task*, improving at longer reaction times. H_1 thus predicts low performance in the absolute orientation task, improving without time pressure, but higher performance in the relative orientation task even at short reaction times. In summary, the two hypotheses predict different main effects under time pressure and an interaction in the form that differences are graded in the absence of time pressure.

To test these hypothesis we calculated the fraction of correct responses separately for each participant and task. Then we performed a 3-way mixed measure ANOVA with performance as a dependent variable, task as a repeated factor (absolute vs. relative), and response mode (3 s vs. infinite) and gender as between participant factors. We decided to include gender in order to account for earlier reported gender difference in the domain of spatial cognition. The test revealed no main effect of the task ($F(1,65) = 2.648$, $p = .109$, partial $\eta^2 = .039$), supporting the assumption that the difficulty in the absolute and relative tasks was comparable. However, we observed a significant main effect for response mode ($F(1,65) = 56.479$, $p < .0001$, partial $\eta^2 = .465$), as well as a main effect of gender ($F(1,65) = 20.968$, $p < .0001$, partial $\eta^2 = .244$). Post Hoc comparions with Bonferroni corrections confirmed that infinite response time, improved performance significantly compared to the 3 s response time ($p < .001$) and that males outperformed females ($p < .001$). There were no interactions of gender with response time ($F(1,65) = .083$, $p = .774$, partial $\eta^2 = .001$) or test condition ($F(1,65) =.585$, $p < .447$, partial $\eta^2 = .009$). The three way-interaction of all factors was also not significant ($F(1,65) = .320$ $p =.859$, partial $\eta^2 < .001$). However, we found an additional significant interaction between test condition and response mode ($F(1,65) = 17.630$, $p < .0001$, partial $\eta^2 = .213$). As a follow up we conducted two separate paired t-tests (one for each participant group) because our goal was to investigate potential differences between the absolute and the relative task, seperatly for the two reponse modes. In fact the Bonferroni corrected test statistics revealed opposite effects: With 3 s response time participants performed significantly better in the relative orientation task ($M=56.04$, $SD=6.38$) compared to the absolute orientation task ($M=52.84$, $SD=6.39$), $t\ (38) = -2{,}418$, $p = .021$). Vice versa, with infinite response time participants showed a significantly higher performance in the absolute orientation task ($M=66.85$, $SD=8.88$) compared to the relative task ($M=60.55$, $SD=7.48$), $t(29) = 3{,}610$, $p < .001$). These results are shown in figure 3 and are fully compatible with H_1. We conclude that our participants had a better access to information on object-to-object relations than on single objects. However, given enough time for cognitive reasoning, performance improved strongly for the absolute task, while performance in judging object-to-object orientation only improved moderately.

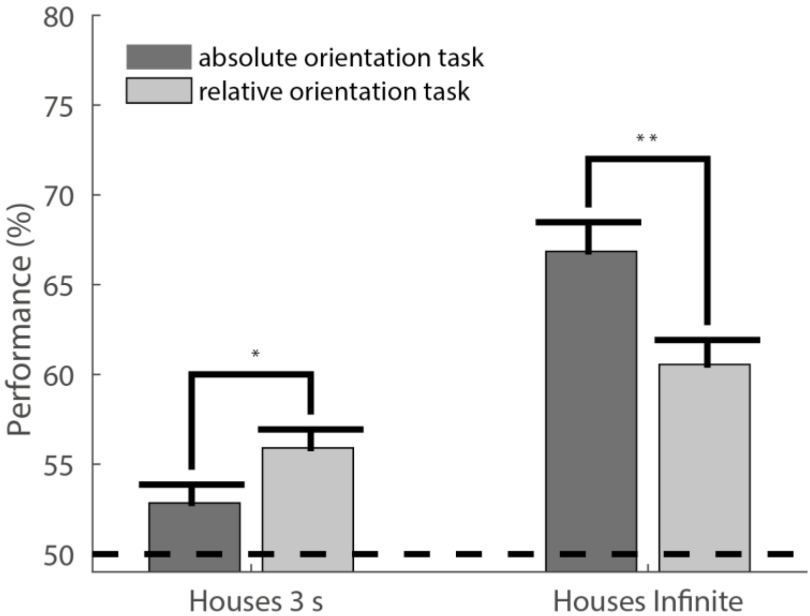

Figure 3: **Absolute vs. Relative orientation task with varying response modes.** The y-axis displays the mean performance levels for the different subtasks. The dark grey bars refer to the absolute orientation tasks, while the light grey bars refer to the relative orientation tasks. The two bars on the left show the performances in the 3 s response mode conditions with house stimuli, while the two bars on the right depict performance levels for the infinite response conditions also using the house stimuli. The chance level (50%) is indicated with the black dashed line. The error bars are Standard Errors of the Mean (SEM) and the asterisks indicate significance at the respective thresholds of $*=p<0.05$ and $**=p<0.01$.

Testing access information relating to single localized objects (houses) and action related objects (streets).

Figure 4: Absolute orientation task with street stimuli. The illustration shows one example trial of the absolute orientation task using street stimuli. Overall, we applied the same principles as for house stimuli. Again, one of the arrows was pointing to the true north cardinal direction while the other was pointing in a different direction in steps of 30°. Also the task of the participants (selecting the arrow that correctly points towards north) remained identical.

Next, we wanted to test (H_2), whether orientation information of objects that are directly relevant for actions, such as streets, is learned differently (*unitary code*) and thus showing a different behaviour than for houses (objects). To answer this question we tested the participants of the second cohort with a different stimulus set showing streets. In general, the absolute orientation task, and the relative orientation task were conducted in the same way as it was done using house stimuli. Specifically, we used the same number of images, and all images were also collected from the Osnabrück city area. In order to compare performance between both stimuli sets we again, performed a mixed measures ANOVA with test performance as the dependent variable, task (relative vs. absolute) as a repeated factor and stimulus set (houses vs. streets) and gender as between participant factors. Neither the task ($F(1,65) = .153$, $p = .697$, partial $\eta^2 = .002$) nor the stimulus set ($F(1,65) < .001$, $p = . 991$, partial $\eta^2 < .001$) revealed a significant main effect. Thus, the absolute orientation task and the relative orientation task were of comparable difficulty and the task demands of estimating the orientation of houses and streets was comparable as well. The factor gender revealed only a significant main effect ($F(1,65) = 18.454$, $p < .0001$, partial $\eta^2 = .221$), but none of its interactions became significant. Again the three way-interaction of all factors was not significant ($F(1,65) = .549$, $p = .461$, partial $\eta^2 = .008$). Importantly, the interaction of the task and the stimulus set reached significance ($F(1,65) = 9.105$, $p = .004$, partial $\eta^2 = .123$). To test where the effect came from, we contrasted the absoute and the relative orientation task seperately for both stimuli sets (Figure 5). As shown before in the time pressure condition, participants jugding the house stimuli showed a significantly better performance in the relative orientation task (M=56.04, SD=6.38) compared to the absolute task (M=52.84, SD=6.39), t (38) = -2,418, p = .021). In contrast, participants jugding street stimuli performed significantly better in the absolute orientation task (M=56.51, SD=6.10) compared to the relative one (M=52.48, SD=7.01), t(29) = 2,414, p = .022). These results suggest that orientation of houses and streets are accessed differently. While object-to-object relations of houses are easier accessible than absolute cardinal information of houses, a streets' absolute orientation is easier to judge than relation of two streets.

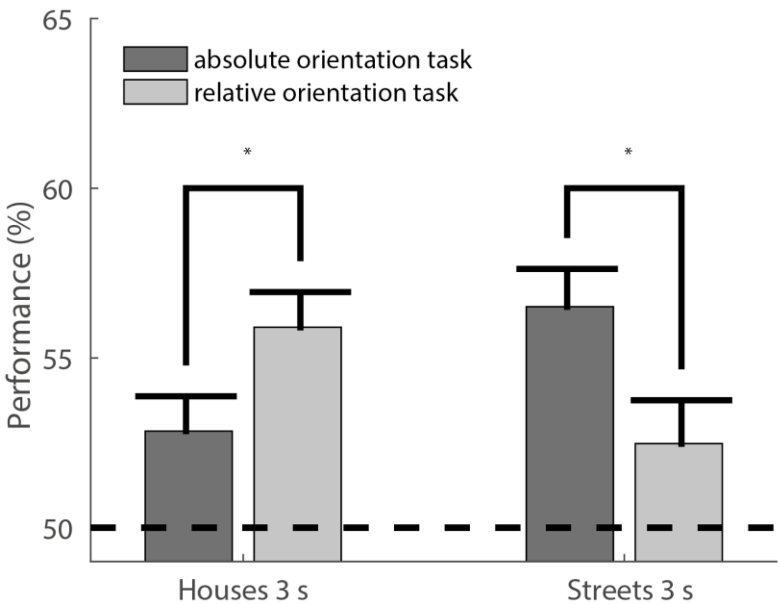

Figure 5: **Absolute vs. Relative orientation task with varying stimuli.** The y-axis displays the mean performance levels for the different subtasks. The dark grey bars refer to the absolute orientation tasks, while the light grey bars refer to the relative orientation tasks. The two bars on the left show the performances using house stimuli and the 3 s response mode condition, while the two bars on the right

depict performance levels using the street stimuli and the 3 s response mode condition. The chance level (50%) is indicated with the black dashed line. The error bars are Standard Errors of the Mean (SEM) and the asterisks indicates significance at the respective thresholds of *=p<0.05.

Relating spatial location between objects – Pointing task

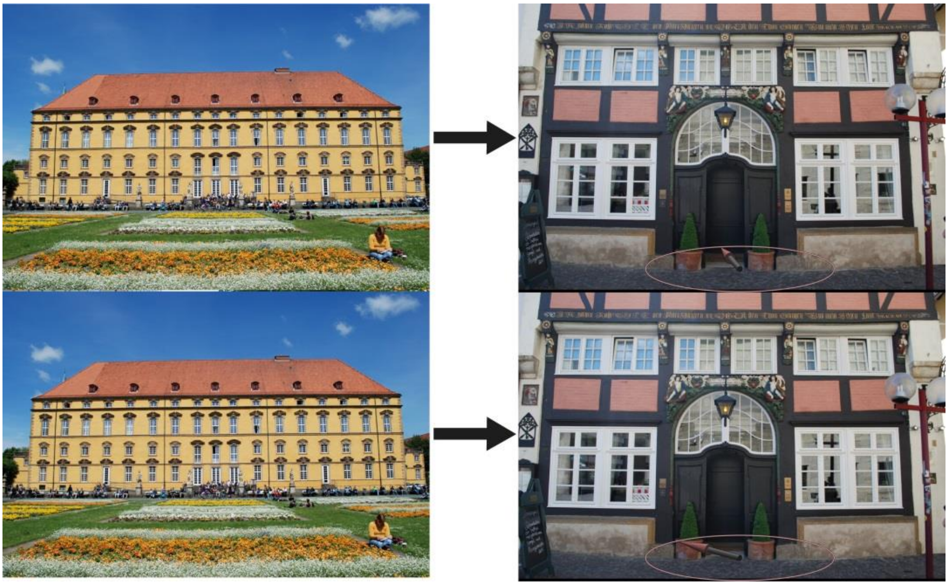

Figure 6: **Pointing Task with house stimuli.** The illustration shows one example trial of the pointing task using house stimuli. Similarly to the relative orientation task, a prime was shown first for 5 seconds and then two target images appeared for 3 seconds. The target images were identical, but the arrows pointed into different directions, providing alternative choices. One of the arrows was (correctly) pointing to the location of the prime, while the other was pointing into a different direction (30° steps). The task of the participants was to select the arrow (image) that correctly pointed back to the prime.

The pointing task was conducted to compare performance levels of our orientation tasks to a more established paradigm that requires knowledge of spatial relation between the location of tested objects. Hence, we measured the ability of participants to select the correct direction from a house towards another house, which was shown as a prime. We used the same stimulus material and selected fixed pairs of images (prime and target image) as beforehand. However, the prime images were different to the relative orientation task. For each of the 144 trials, first the prime stimulus appeared (on both screens) for 5 seconds and after its offset the target stimulus appeared again on both screens. Similar to the absolute alignment task, we overlaid each target image with an ellipsoid, including a pointing arrow. One of the arrows was correctly pointing into the direction of the prime image location, the other arrow was pointing into a different direction with varying degrees (0-330° in 30° steps). The task of the participant was to choose the image where the arrow pointed correctly towards the prime stimulus by pressing either the up or down key respectively. Comparable to the *absolute orientation task*, a *unitary code* (H_0) requires separate access to the information of both houses and, some additional cognitive reasoning to achieve the *object-to-object pointing task*. Thus, a *unitary code would* result in a low performance in this task. In contrast, given a *binary code* (H_1) the required information of object-object relation is directly accessible. As object location refers more directly to action than an objects' orientation, H_1 predicts an even higher performance as in the *relative orientation task*, even at short reaction times. Keeping stimuli sets and response mode identical, we then compared the pointing performance to the performance of the absolute and relative task of the first cohort. Hence for statistical testing we conducted two separate one-way ANOVAs, comparing pointing performance to the two orientation tasks described above, which also used the houses stimuli and 3 s response mode. As shown in Figure 7, performance in the pointing condition was highest among all three tasks. In fact, pointing performance was significantly higher compared to the absolute orientation task ($F(1,68) = 14.256$, $p < .0001$, partial $\eta^2 = .175$). However, the difference to the relative task performance did not reach significance ($F(1,68) = 3.621$, $p = .061$, partial $\eta^2 = .051$). Our results indicate that knowledge about object-to-object relations and about object-to-object orientations are significantly better than estimate of absolute object orientations but yield no significant difference between each other.

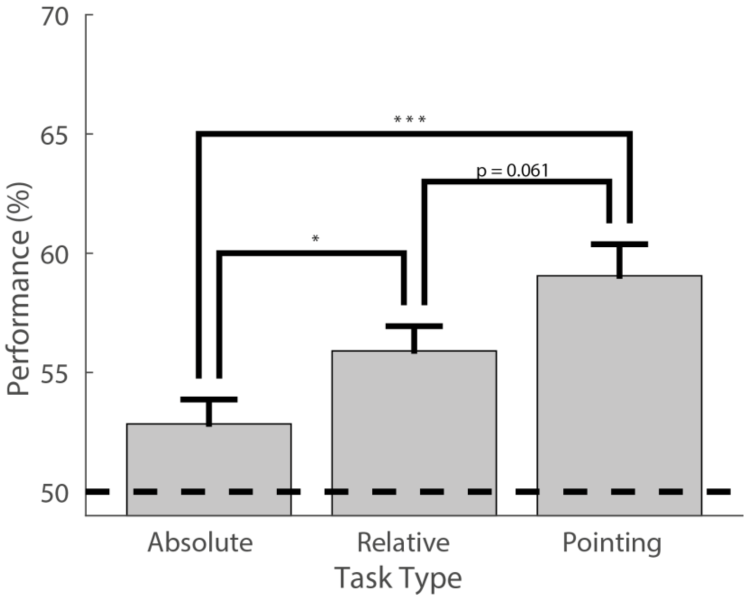

Figure 7: Comparison of orientation and pointing tasks. The y-axis displays the mean performance levels for the different subtasks using house stimuli and the 3 s response mode. On the x-axis the leftmost bar shows the performance of the absolute orientation task, the central bar shows the performance for the relative orientation task and the rightmost bar shows the performance of the pointing task. The chance level (50%) is indicated with the black dashed line. The error bars are Standard Errors of the Mean (SEM) and the asterisks indicate significance at the respective thresholds of *=p<0.05, **=p<0.01 and ***=p<0.001.

Familiarity with the Objects

In order to strengthen the claim that our participants learned the relation of real world objects due to active behavior (i.e. walking through the city), we aimed to investigate how much individual experience and exposure with those real world objects influenced the participants' behavior. Hence, we requested all participants to rate their individual familiarity for each stimulus on a Likert scale (1-7). For the respective analysis, we then first z-transformed the familiarity ratings for each participant such that individual biases, preferring overall higher or lower scorings, were removed. Next, we applied a Generalized Linear Model (GLM) to all the data, separately for each of the different subtests. Here, the binominal responses (correct, wrong) were fitted against the different levels of familiarity using a logit link function. The results of the analysis are summarized in Table 2. The results for the absolute orientation task show that our participants needed time in order to profit from "being familiar" with the object, supporting the notion that high performance in the infinite time task is supported by elaborate cognitive reasoning. Interestingly, the results of the relative orientation task were slightly different. In particular, when having only a limited time to respond the participants showed a positive correlation of performance and the correct target, but a negative correlation of performance and the incorrect target. In other words, the participants tended to pick the object, which was more familiar to them when having only a limited amount of time. However, this changed again when the response time was infinite. In that situation knowing both the correct and the incorrect target helped to increase performance. Overall these results support the idea that active navigation behavior leads to improved object-to-object representations.

Influence of Object Familiarity							
Task Type	**Response Mode**	**Stimulus Type**	**Target**	**Beta(2)**	**T-stat**	**df**	**p**
Absolute	3 s	Houses	-	-0.037	-1.280	4829	.2002
Absolute	3 s	Streets	-	-0.095	-2.7708	3301	.0070
Absolute	Infinite	Houses	-	-0.287	-8.6070	4228	< .0001
Relative	3 s	Houses	Correct	-0.188	-4.0999	2018	< .0001
			Wrong	0.265	5.6402	2018	.0006
Relative	3 s	Streets	Correct	-0.227	-4.3202	1504	< .0001
			Wrong	0.202	3.81905	1504	< .0001
Relative	Infinite	Houses	Correct	-0.327	-6.3773	1798	< .0001
			Wrong	-0.052	-1.0892	1798	.2761

Table 1: Statistical Results of the Familiarity Analysis. The different columns separate the results for the different subtests; the first 3 rows show the results for

the absolute orientation tasks. As we separately analyzed the influence of the correct and the incorrect stimuli for the relative task, there are 6 different rows (row 4-9) for the relative orientation task. The first column illustrates the task type, the second column shows the response mode, while the third depicts the stimulus set. The forth column is only used by the relative orientation task to differentiate between correct and incorrect target image. Column five to eight show the test statistics: Column five shows the beta (2) value of the logistic fitting function which describes the slope of the sigmoidal fit; column six shows the t-value of the fit, column 7 displays the degrees of freedom and column eight illustrates the corresponding p-value. All tests with a significant result are highlighted with grey background.

Angular Difference

The key question of our study investigates how people learn and represent absolute (cardinal) and relative (object-to-object) differences of orientation between real world objects. In order to evaluate whether our introduced experimental manipulation, namely the difference in orientation between two real world objects, had an influence on the participants' performance, we grouped the stimuli accordingly in bins of 30°. Similar to the familiarity analysis, we then applied a Generalized Linear Model (GLM) to all the data, separately for each of the different subtests. The binominal responses (correct, wrong) of the participants were fitted against the different levels of angular difference, also using a logit link function. Overall, the effect size was rather weak, meaning that larger angular differences of two stimuli did not always (for each participant and condition) result in better performance. In particular, the two subtests which had an overall very low, near chance performance (i.e. absolute houses 3 s and relative streets 3 s) showed no such psychometric behavior. As a result individual psychometric evaluation could not be realized. However, in accordance to the previous findings, all other conditions that showed an overall reasonable performance (>55%), demonstrated a significant ($p<0.05$) change in slope. Hence, we can conclude that on a grand average scale, larger angular differences between two objects led to better performance.

Influence of Viewing Direction

Hegarty and colleagues suggested that the alignment of viewing direction and true cardinal direction can have a strong impact on spatial judgments (Hegarty, Eds, & Goebel, 2014). Hence, we aimed to find out whether the deviation of the viewing direction with true north, indicated by arrow direction, also influenced our participants' decisions. Therefore, we first calculated the average performance for each stimulus as a mean across participants, separately for the different subtests. Then, we analyzed the performance as a function of the difference between the viewing direction and true north. Specifically, we determined the direction that resulted in the best performance. To account for the circular nature of cardinal direction information, we then fitted a cosine to the data and as a result got the phase φ which yielded the best fit as well as the explained variance of the fit (R^2). We performed this analysis for both the relative and the absolute orientation task; however as none of the relative task conditions revealed any effects, we consequently report only the details for the absolute tasks. Figure 8 shows that the performance of the two fast response mode conditions (absolute houses 3 s, absolute streets 3 s) was clearly modulated by an alignment of the viewing direction and true north. The best fit for the absolute houses 3 s condition was achieved very close to the full circle with φ=359.28, reaching an R^2 of 0.287. The best fit for the absolute streets 3 s condition had an φ=9.52° having an R^2 of 0.301. In a second step, we tested for statistical significance, and consequently divided the data in two bins: In the first bin we put all stimuli in which the correct arrow (north) pointed in the forward direction (270°-90°); while in the second bin we put the remaining stimuli with the correct arrow pointing backwards. Consequent one-way ANOVAs showed that performance was significantly higher in the first bin, for both absolute houses 3 s ($F(1,139) = 36.930$ $p < .0001$, partial $\eta^2 = .211$) and absolute streets 3 s ($F(1,142) = 57.337$, $p < .0001$, partial $\eta^2 = .289$). In summary, participants performed best, when the correct (true north) arrow was pointing right in front of them, therefore being aligned with their own viewing orientation. Interestingly, this effect was most visible when decisions under time pressure (3 s response mode) were required. With infinite amount of response time the size of the effect decreased dramatically, yielding a poor circular fit ($R^2 = 0.014$) as well as borderline significant difference ($F(1,140) = 4.065$, $p = .046$, partial $\eta^2 = .028$).

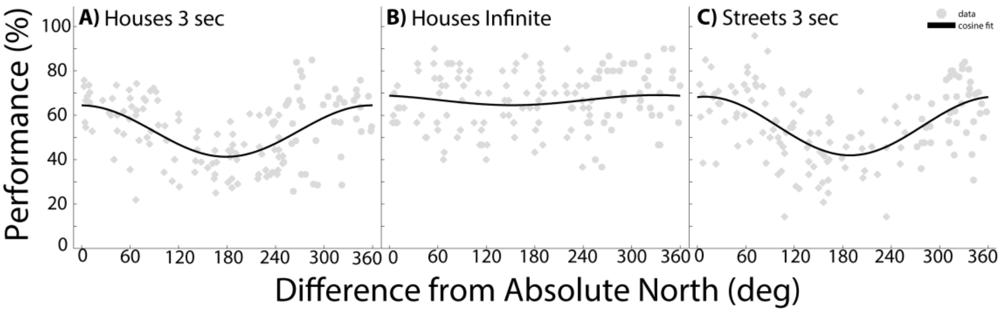

Figure 8: Influence of viewing direction for the absolute orientation tasks. The three panels show the influence of viewing direction for the various absolute orientation tasks. The left panel shows the data for the houses 3 s condition, the center panel shows the data for the houses infinite condition, and the right panel shows the data for the streets 3 s condition. The y-axis displays the average performance for each image as a mean across participants. The x-axis indicates the difference between the correct north cardinal direction (pointing direction of the correct arrow) and the viewing direction for each image. Each light grey dot represents one image with a certain average performance level, while the curved black lines indicate the best possible cosine fit of the data. The highest peak of the fitting curve indicates the angle that led to the overall best result.

4.4 Discussion

In the present study we investigated how spatial information about orientation and location of houses and streets is coded. We performed three different experiments requiring spatial orientation abilities, additionally varying stimulus material and response mode. Our results show a significantly better performance in assessing the relative orientation of houses to each other (binary code, H_1) than rating their individual cardinal orientation (unitary code, H_0) when spontaneous knowledge retrieval was required. This result, that relative object-to-object orientation yields better performance than individual object orientation to cardinal directions, is compatible with coding of houses in a perspective-free allocentric representation and supports the hypothesis that also non-egocentric spatial knowledge is learned action oriented. Indeed, enduring memories of object locations in the environment are represented in parts in terms of allocentric reference frames (Burgess, 2008; Hodgson, 2006; Meilinger & Vosgerau, 2010; Mou & McNamara, 2002; Mou, McNamara, Rump, & Xiao, 2006; Sargent, Dopkins, Philbeck, & Modarres, 2008).

Furthermore, this line of argument is supported by our observation that the pointing task, which directly probes action relevant knowledge of how to get from one location to another, revealed an even higher performance than cardinal orientation tasks. The possibility of using cognitive strategies (infinite response time) enabled participants to strongly improve their judgments of houses' cardinal orientation, but influenced relative task performance much less. Furthermore, in contrast to houses, we provide evidence that streets are preferentially coded in a unitary code (cardinal orientation), even when retrieval time was restricted (H_2). However, streets are not localized objects such as houses but are better described by a vector. Thereby, streets inherently represent a relation between locations, for example the means how to get from house A to house B. Hence, what is relative information for houses is absolute information for streets. Thus, the coding of street orientation is compatible with the classical allocentric reference frame. The reverse findings for our house and street stimuli with different variants of allocentric reference frames thereby further support the idea that spatial information is learned in an action oriented way. In summary, our results indicate that people learn real world object-to-object relationships in an action oriented way.

Potential shortcomings of the study

Using real world stimuli imposed several obstacles to both the experimental design and the analysis. First of all, the stimulus selection was somehow influenced by the experimenter. However, due to the rather small size and unique structure of the Osnabrück city center, such a selection process followed a natural schema (i.e. there are roughly 150-200 buildings that are more or less known to all inhabitants). Furthermore, the recording conditions of different photographs were not absolutely identical (some pictures were taken on midday, some on late afternoon). However, the resulting small differences in i.e. lighting conditions were unlikely to interfere with the observed effects. Additionally, for the relative orientation task, we had to group the stimuli according to their cardinal facing direction. But due to the real world nature, no two houses or streets were oriented exactly identical. Hence, we were not able to determine the effect of relative orientation with arbitrary precision. However, the analysis of angular difference (applying a GLM) clearly showed that increasing angular difference was noticed and in general led to higher accuracy. Finally, experience with the real world objects might have differed between participants leading to a difference in familiarity. However, to ensure some similarity of preexisting experiences as a constraint we only included participants if they had lived at least one year in Osnabrück prior to the start of the study. Additionally, we recorded the familiarity for all participants and each individual object but did not find strong differences between the individual ratings. Another point worth discussing is our fractional design. The two different cohorts performed different tasks, which prevented us from performing one omnibus statistic. However, testing the same participant in the same task once with time pressure and once without time pressure would have caused difficult carry over effects. Performing all tests with all participants would also have caused that the experimental sessions take more than 3 hours, which is not feasible. Hence, our fractional design was chosen on purpose and insured a better experimental control. A last issue of concern is the size of the observed effects. Arguably, the overall performance levels are rather weak in both orientation tasks, in particular when participants only had 3 seconds to respond. However, the sample sizes for both cohorts were rather large (39 and 30) so that the effects could be defined with a lot of statistical power and certainty.

Gender effects and familiarity influences

In order to better understand our data and to avoid overseen alternative interpretations, we included several other factors in our analysis. First, situated in the realm of spatial cognition, we decided to investigate whether gender played a role in the present study. Our results clearly support the view that males outperformed females in most of the tasks. This is in line with several former studies attributing both faster reactions and higher performance to males in a variety of spatial tasks (Masters & Sanders, 1993; Moffat et al., 1998; Newhouse et al., 2007; Woolley et al., 2010). However, in none of our test results, we found a significant interaction including the factor gender. In other words, while there was a general performance offset between males and females, the relative performance between tasks was identical for both genders. This implies that the findings are valid for both males and females, which again strengthens the reported results. Second, we aimed to analyze how much individual knowledge about the tested objects influenced our findings. In line with Bethell-Fox and colleagues (Bethell-Fox & Shepard, 1988) who reported that mental rotation performance was highly dependent on object experience, our results of the influence of object familiarity also demonstrated clear effects. When two different objects were shown (relative orientation task) and the response required fast, implicit decision making, participants were more likely to pick the object that was more familiar to them. This can be seen as some kind of shortcut strategy. However, more interesting is the fact that with enough time to rely on cognitive reasoning, familiarity improved performance in both tasks. This leads to the conclusion that information of object orientation is part of our episodic memory, which is again experience and action dependent.

Mental Rotation and Alignment Effects

Wraga and colleagues (Wraga, Creem, & Proffitt, 1999) showed that mental rotations of oneself around an object are easier and lead to better recognition performance than when the own viewing perspective is fixed while mental rotation of an external object is required. These results are highly compatible with an enactivist view of spatial cognition as during real world active navigation humans very often walk or drive around houses, but it rarely happens that houses or other large objects are rotated around their axis. Sholl and colleagues (Sholl, 2008; Sholl, Kenny, & DellaPorta, 2006) performed an allocentric-heading recall task and showed that the alignment of the participant's current physical heading and the perspective of a given photograph improved decision speed. Burte and Hegarty (Burte & Hegarty, 2012) confirmed these findings and additionally showed a correlation of the alignment effect and general spatial abilities. Furthermore, spatial relations can be learned from experience but also from maps (Richardson, Montello, & Hegarty, 1999; Sun, Chan, & Campos, 2004). For example, pointing task in virtual Tübingen revealed that participants used a mental map of Tübingen that was oriented north (Frankenstein et al., 2012), but used local reference frames (LRF) encoded parallel to the orientation of local streets while walking for estimating route decisions to a goal (Meilinger, Frankenstein, & Bülthoff, 2013). This suggests that spatial memory can be acquired from maps and online while navigating (McNamara, Sluzenski, & Rump, 2008; Meilinger, 2008; Wang & Spelke, 2002) and reference frame orientation organizes accordingly.

In line with these previous studies, in the absolute orientation task of the current study participants performed best when the north (correct) arrow was pointing right in front of them, while performance decreased (circularly) with growing angular distance(Frankenstein et al., 2012). However, in the present study we explicitly modified the response time parameter and found that the effect was only visible, when spontaneous decisions (3 s response time) were required. One possible interpretation from an enactive point of view is the idea that participants need to align the arrow with the implied viewing direction in order to solve the task. In other words, people can only judge whether an arrow is pointing north if they can see or imagine what is right in front of the arrow. This would require mental rotation of the scene (image) towards the direction of the arrow. However, larger mental rotations take more time to be carried out correctly, such that the participants had enough time in the infinite response mode, but did not have enough time in the spontaneous response mode.

Reference Frames and Enactivism

The concept of spatial reference frames has been vastly studied throughout the last decades (Goeke et al., 2015; Goeke et al., 2013; Gramann, 2013; Klatzky, 1998; Riecke et al., 2007) In human studies the concept of spatial reference frames has mostly been centered on ego- and allocentric reference frames thus simplifying a more divers field (Redish & Touretzky, 1997; Touretzky & Redish, 1996). These studies reported interesting differences in the usage of ego- and allocentric reference frames. Extending this dichotomous division, Diwadkar and McNamara (Diwadkar & McNamara, 1997) as well as Shelton and McNamara (Shelton & Mcnamara, 1997) defined a concept of an intrinsic reference for objects combining egocentric and environmental cues that are actively learned (McNamara, 2002; McNamara et al., 2003). They showed that humans rely on these intrinsic reference frames when they have to remember spatial layouts. Several other studies replicated and extended these findings (Mou, Fan, McNamara, & Owen, 2008; Mou & McNamara, 2002; Shelton & McNamara, 2001). In essence, all these studies demonstrated that recognition performance of spatial layouts is higher when the viewing-perspective of training and test phases were identical. Hence, these authors concluded that the way we learn and memorize (non-egocentric) multi-object configurations is dependent on individual viewing perspectives during the learning phase. In that respect, it is important to mention that the perspective from which the photographs of the present study were taken from a canonical perspective and supposedly similar to the learning phase (during real world navigation) and the test situation for all participants. In particular, the photographs were taken from the navigator’s perspective, as if one just enters a building or walks on a street. Thus, our experimental design is ideal to study how intrinsic references are learned in a real world scenario. Recently, Frankenstein and colleagues (Frankenstein et al., 2012) tested pointing performance without time constraints and found that performance was best when participants were facing the north direction. Our results show a similar (alignment) effect, but only under time pressure and only for the absolute orientation task. Importantly, here we also show that (under time pressure) judgments of cardinal directions are worse than judgments about object-to-object relations. A single, north oriented, reference frame learnt by (inactive) studying of a city map cannot explain these findings. Instead, the pattern of results suggests that people learn implicitly how two (or more) intrinsic reference frames are related during active navigation. At this step (absolute) cardinal information is irrelevant. In a later, cognitive step, this knowledge can then be used to derive information about cardinality and develop a map like (north centered) representation.

Spatial Cognition and Sensory Motor Contingencies

In 2001 O`Regan and Noë (O'Regan & Noe, 2001) brought forward the paradigm of sensorimotor contingencies (SMCs) within the framework of Enactivism. Sensorimotor contingencies are defined as lawful dependencies between actions and associated perceptions that are learned while interacting with the environment. As the rules that are learned differ between modalities, SMCs are modality specific (O'Regan, 2011; O'Regan & Noe, 2001). Since it was originally formulated the SMC paradigm has broadened. Maye and Engel (Maye & Engel, 2012) suggested long-term regularities of action sequences beyond the time scale of object perception "like driving to work or baking a cake" that they called "intention-related" SMCs. They developed a computational model of SMCs with the basic idea to regard "SMCs as multistep, action-conditional probabilities of future sensory observations" (Maye & Engel, 2011). This model was tested on a robot that controlled the locomotion by developing perceptual capabilities and enabled successful navigation within a task environment (Engel et al., 2013). Interpreting our results in the light of such an SMC framework, we argue that humans learn action relevant associations of objects in terms of their relative orientation and location while walking through the urban environment. This helps to make correct decisions even under time pressure, as seen in our relative orientation task. Knowing the exact location or orientation of an object (independent of the navigators' current position and orientation) is irrelevant for action. Hence, it takes time and requires cognitive operations to calculate the cardinal reference frame, which was needed to solve the absolute orientation task. In summary, the concept of sensorimotor contingencies constitutes a valid and convincing framework to explain the results obtained in this study.

Conclusion

The present study investigates coding of allocentric information of different types of objects relative to a cardinal direction as well as relative to each other. The results suggest that human participants use classical allocentric as well as perspective-free allocentric reference frames, depending on the nature of the object and its relation to action. At leisure time these differences are evened out or even reversed. This pattern of results supports the view that spatial information about object orientation and location is primarily learned in an action oriented way as proposed by an enactive framework for human cognition

4.5 Materials & Methods

Stimulus Recordings & Preparation

Overall, we used two different stimuli sets, real world photographs of houses and of streets taken in the Osnabrück city area. All photographs were taken using the same camera (type) and used the same camera settings. The distance to the objects was set between 5 and 15 meters depending on the viewpoint that resulted in the most intuitive perspective (i.e. such that the whole object was visible). While taking the photos, we avoided various weather or lightning conditions (rain, darkness) and also made sure no other objects or people occluded the main object. All photos were taken in front-on fashion such that for houses the viewing direction of the photo was aligned with the facade of the object (see Figures 1-2). Regarding streets we only picked straight segments such that the viewing perspective was straight along with the street view (see Figure 4). The recording of the cardinal direction was conducted using a mobile phone, in parallel with the taking the pictures. In order to avoid outliers regarding these recordings (e.g. electromagnetic disturbances) we took 5-7 measurements of cardinal direction for each photograph and later on calculated the average. For both the relative orientation task and the pointing task, we selected fixed sets (pairs and triplets) of images that were presented together within one trial. The selection of the prime images for both tasks was based on a pilot study (8 participants) in which all participants rated the familiarity all stimuli. The most famous images were chosen as prime images. Additionally, for the relative orientation task, we applied an optimization algorithm that selected the target images such that the cardinal direction of the correct target image was very closely aligned to the orientation of the prime image (<10°) while the orientation of the incorrect target image varied in cardinal facing direction compared to the correct target in roughly equal steps from 0° to 330° for each image.

Training & Familiarity Judgments

Each participant performed a response training, in which they trained first to respond within 3 seconds and then learned to dissociate arrow-pointing direction on the screen and required behavioral response. In this training, one ellipsoid was presented on the upper and one on the lower screen. In each ellipsoid one arrow was pointing into a particular direction. The participants had to compare the two arrows and then select either the arrow on the upper screen (upper button) or the arrow on the lower screen (lower button) depending on which of the two arrows was pointing more straight (upwards). On each trial they got feedback whether they decided correctly (green frame), wrong (red frame) or even failed to respond in time (blue frame). In order to finish the training the participants had to respond correctly without misses 48 times in the last 50 trials (95%). With this pretest training the reaction of the participants' was practiced thus enabling them to press the correct button also with limited time. At the end of the recordings, each participant rated the stimuli according to their individual familiarity (Likert 1-7). The second cohort who performed tests with both stimuli sets (houses and streets) rated the familiarity for both sets separately.

Participants & Procedure

Overall we recruited 69 participants who at least have lived one year in Osnabrueck. However, due to task complexity, amount of trials and possible carry over effects we performed the experiment in two cohorts. Cohort 1 included 39 participants, with 24 females and a mean age of 24.2 years (SD= 2.47 years).

Cohort 2 included 30 participants with 19 females and a mean age of 23.3 years (SD= 2.34 years). Most importantly, we modified two parameters for our experiments between these two cohorts, stimulus mode, and response mode. The two stimulus modes were houses and streets while the two response modes were either 3 seconds or infinite amount of time. The first cohort performed the absolute and the relative alignment task with the house stimuli in the 3 seconds response mode. The second cohort performed the absolute and relative alignment task with street stimuli in the 3 seconds response mode and with house stimuli in the unrestricted time condition. The second cohort additionally conducted the pointing task with houses as stimuli and 3 seconds response mode. A summary of the tasks can be found in table 2. During the whole experiment all participants sat in approximately 60 cm distance to a six screen monitor setup. However, the images were presented only on the two central screens (above each other), while the other four monitors were switched off. The resolution of the original images was 3872x2592 pixels, but all photographs were rescaled such that each image was presented in full screen (2160x1920 pixels) on one of the monitors. Each participant started with the training task and performed the familiarity raining(s) at the end of the recordings. The order of the other subtasks, as visible in table 1, was balanced across participants such that any remaining carry over effects would have cancelled each other out. The order of stimulus presentation for each task and recording was also randomized and each participant was presented with a different sequence of the stimuli. All participants were informed about the task and filled out the required consent form. Ethical IRB approval was obtained prior to the recordings from the ethics committee of the University of Osnabrück. The participants were either reimbursed with 7 Euros per hour or earned an equal amount of “participant hours”, which are a requirement in most students’ study programs. Overall, an experimental session in cohort 1 took about 1 hour and in cohort 2 about two and a half hours.

Cohort	Task / Experiment	Stimulus Type	Response Mode
1	Training	Arrows	3 sec
1	Absolute Alignment (1)	Houses	3 sec

1	Relative Alignment (2)	Houses	3 sec
1	Familiarity Rating	Houses	Infinite
2	Training	Arrows	3 sec
2	Absolute Alignment (1)	Streets	3 sec
2	Relative Alignment (2)	Streets	3 sec
2	Absolute Alignment (1)	Houses	Infinite
2	Relative Alignment (2)	Houses	Infinite
2	Pointing (3)	Houses	3 sec
2	Familiarity Rating	Houses	Infinite
2	Familiarity Rating	Streets	Infinite

Table 2: Overview of the complete study task design

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5. Study Four: The FeelSpace Study

This study is currently in press at “Plos-One”

Learning New Sensorimotor Contingencies: Effects of Long-term Use of Sensory Augmentation on the Brain and Conscious Perception

König, S. U., Schumann, F., Keyser, J., Goeke, C., Krause, C., Wache, S., … Peter, K. (in press).

5.1 Abstract

Theories of embodied cognition propose that perception is shaped by sensory stimuli and by the actions of the organism. Following sensorimotor contingency theory, the mastery of lawful relations between own behavior and resulting changes in sensory signals, called sensorimotor contingencies, is constitutive of conscious perception. Sensorimotor contingency theory predicts that, after training, knowledge relating to new sensorimotor contingencies develops, leading to changes in the activation of sensorimotor systems, and concomitant changes in perception. In the present study, we spell out this hypothesis in detail and investigate whether it is possible to learn new sensorimotor contingencies by sensory augmentation. Specifically, we designed an fMRI compatible sensory augmentation device, the *feelSpace* belt, which gives orientation information about the direction of magnetic north via vibrotactile stimulation on the waist of participants. In a longitudinal study, participants trained with this belt for seven weeks in natural environment. Our EEG results indicate that training with the belt leads to changes in sleep architecture early in the training phase, compatible with the consolidation of procedural learning as well as increased sensorimotor processing and motor programming. The fMRI results suggest that training entails activity in sensory as well as higher motor centers and brain areas known to be involved in navigation. These neural changes are accompanied with changes in how space and the belt signal are perceived, as well as with increased trust in navigational ability. Thus, our data on physiological processes and subjective experiences are compatible with the hypothesis that new sensorimotor contingencies can be acquired using sensory augmentation.

5.2 Introduction

In recent years, theories of cognition underwent profound development in cognitive science (Engel et al., 2013). Classical views propose that cognition is precipitated by an internal representation of the outer world shaped by experience (Marr, 1982). This theoretical framework of cognition, however, fails to satisfactorily explain many aspects of cognition (Clark, 1999). As a consequence, the developing paradigm of embodied cognition attempts to provide an appropriate and productive framework.

The paradigm of embodied cognition defines cognition as embodied action (Barsalou, 2008; König, Wilming, Kaspar, Nagel, & Onat, 2013; Varela et al., 1991; Wilson, 2002). Even though the approach of embodied cognition involves divers notions (Clark, 1999; Varela et al., 1991; Wilson, 2002; Ziemke, 2003), here cognition is understood as an activity that includes mind, body, and environment (Clark, 1999). Specifically, cognitive processes are conceived as being rooted in the body's interactions with the world involving perception and action (Wilson, 2002). Embodied cognition in general is theorized as an active and multisensory probing of the environment (Mangen & Velay, 2010).

Within the framework of embodied cognition, O'Regan and Noë (O'Regan & Noe, 2001) formulated the sensorimotor theory of conscious perception. Sensorimotor theory suggests that learning and mastery of systematic relations of action and associated sensory information, called sensorimotor contingencies (SMC), are constitutive of conscious perception. These "rules or regularities relating sensory inputs to movement, changes and actions" (Clark, Tower, & Square, 2006) have to be actively learned. The systematic relations between motor action and associated changes of sensory input of modality and object-related SMCs are learned by acting in the world, and concomitantly shape how we perceive the world.

The theory of SMCs is supported by experimental work in the field of sensory substitution. Sensory substitution strives to provide missing or lost sensory information of a specific modality by another substituting modality. In recent years, many studies provided evidence that the brain is able to functionally and structurally adapt throughout life to altered afferent input, to novel experiences due to environmental changes, and to the learning of new skills (Amedi et al., 2007; Pascual-Leone, Amedi, Fregni, & Merabet, 2005; Proulx, Ptito, & Amedi, 2014;

Ptito, Kupers, Lomber, & Pietrini, 2012). Already in 1969, Bach-Y-Rita and his colleagues (Bach-y-Rita et al., 1969) reported that the adult human brain is plastic enough for blind participants to learn how to use a tactile sensory substitution system to perceive visual input and thus recognize and localize objects in the environment. Since then, these results were supported by numerous experiments using vision-to-tactile substitution (Sampaio, Maris, & Bach-y-Rita, 2001), or other sensory substitution devices like vision-to-auditory substitution (Abboud, Hanassy, Levy-Tzedek, Maidenbaum, & Amedi, 2014; Levy-Tzedek, Hanassy, Abboud, Maidenbaum, & Amedi, 2012), and vestibular-to-tactile substitution (Tyler, Danilov, Bach-Y-Rita, & Medicine, 2003). Learning how to use a sensory substitution device needs time. While subjects learn some perceptual aspects of the substituted stimulus in a very short time, prolonged training with the device develops a more detailed perception (Auvray et al., 2007; Bermejo, Di Paolo, Hüg, & Arias, 2015; Ward & Meijer, 2010). However, it has been argued that no true substitution is achieved, and that acquired skills are better described by the analogy to reading (Deroy & Auvray, 2012). Thus, aspects of substituted as well as substituting modality continue to be relevant. Furthermore, this learning of a new percept much depends on subjects' active exploration and manipulation with the sensory substitution device improving the richness of the perception with increased quality of the sensation and the action (Lenay, Gapenne, Hanneton, Marque, & Genouëlle, 2003). In line with the SMC theory, the reported perception that was mediated by sensory substitution grew in detail with prolong training duration and active handling of the device.

With the rapid progress of molecular biology even augmenting sensory perception is no longer a theoretical question. It is possible to equip mice with the tool set for color vision (Jacobs, Williams, Cahill, & Nathans, 2007) or rats with a magnetic sense (Norimoto & Ikegaya, 2015), thus providing them with the means for a new sense. Given this background, the question arises whether humans can learn to perceive sensory information that is not natural in humans. We previously explored this hypothesis using a specially designed sensory augmentation device, called the *feelSpace* belt (Kärcher, Fenzlaff, Hartmann, Nagel, & König, 2012; Kaspar et al., 2014; Nagel et al., 2005; Schumann, 2012). This device mediates information of magnetic north via continuous vibrotactile stimulation around the waist. Thus, it provides directional information for which humans do not have a natural sensory modality. Sensing the magnetic field is common in the animal kingdom (Mora, Davison, Wild, & Walker, 2004; Mouritsen & Ritz, 2005; Ritz, Dommer, & Phillips, 2002), but has not been reliably observed in humans. Kaspar et al. (Kaspar et al., 2014) showed by evaluating subjective experiences that training with the belt did not lead to a perception of the magnetic field but instead to highly differentiated changes in perception of space of the participants. These perceptual changes included the specific perception of spatial relations of self and objects, an alignment towards cardinal directions that developed to a new feature of objects, and in many participants, to an enlargement of a mental map. Eight out of nine belt wearing participants reported the development of a new sense of spatial perception, which was not found in control participants (Kaspar et al., 2014). Furthermore, the belt's information could be used in a meaningful way in addition to sensory information that is normally used for navigation, such as visual and vestibular information (Foulke, 1971; Emerson Foulke, 1982; Loomis et al., 1993). Even though perceptual and behavioral changes elicited by sensory augmentation are compatible with the SMC theory, four central aspects are still unresolved.

Therefore, in the present study, we used the *feelSpace* belt to develop a deeper understanding of sensory augmentation and test the theory of SMCs. First, to develop SMCs new sensory input provided by an augmentation device has to be actively learned. Therefore, we aimed to obtain insight into the learning process that is involved in using the *feelSpace* belt. As SMC theory predicts that learning and mastering a novel sensorimotor contingency is not dependent on cognitive deliberation, we hypothesize that it involves a procedural learning process. During procedural learning sleep has a beneficial role in processing the information obtained during wakefulness and subsequent memory consolidation (Walker & Stickgold, 2004). In particular, both in humans (Maquet, 2001; Smith, 2001) and in animals (McGaugh, 2000; Smith, 1995) rapid eye movement (REM) sleep is the most beneficial type of sleep for consolidation of procedural memory (Smith, 1995; Smith, 2001). Furthermore, intense periods of procedural learning lead to an increase of power in the sigma frequency range during stage 2 sleep and slow wave sleep (SWS) (Fogel, Smith, & Cote, 2007). Accordingly, we hypothesize that training with the *feelSpace belt* will induce a procedural learning process that is reflected by an increase of REM sleep duration as well as by an increased EEG sigma power during sleep, especially in the early training period.

Second, SMC theory predicts that sensory processing cannot be studied in isolation, but by necessity involves motor structures. Thus we hypothesize that learning of the new sensory signal with the *feelSpace* belt induces observable and specific changes in neuronal activity in sensory as well as motor cortex. A number of studies demonstrate neuronal plasticity in healthy subjects through extensive training. For example, right-handed violinists displayed a spatially more extended cortical region relating to the intensively trained left hand while practicing the violin (Schwenkreis et al., 2007). Similarly, the investigation of London taxi drivers revealed a larger hippocampus associated with their huge amount of navigational abilities and map knowledge (Maguire, Frackowiak, & Frith, 1997). Several studies examining learning and use of sensory substitution devices (Amedi et al., 2007; Ptito, Moesgaard, Gjedde, & Kupers, 2005; Striem-Amit, Dakwar, Reich, & Amedi, 2012) in sighted and blind humans observed physiological changes in brain activation patterns with cross-modal activation and activation of higher cortical areas. Along similar lines, we compare the brain activity before and after the training with the *feelSpace* belt in a fMRI paradigm. As the concept of mastering SMCs proposes a direct relevance of motor action for processing of sensory information, we hypothesize that learning to utilize the *feelSpace* belt as a sensory augmentation device involves not only low-level somatosensory areas but also higher order motor centers and areas that are involved in navigation. Specifically, acquiring and mastering the belt's information will induce changes in brain activity involving higher motor centers, such as supplementary motor area and posterior parietal cortex, and brain regions participating in navigation, like the nucleus caudatus, and the hippocampus.

Third, we hypothesized that once the new sensory input is mastered; it can be actively used and is observable in behavioral tasks. Path integration, firstly postulated by Charles Darwin (Darwin, 1873), enables homing back to the starting position during the exploration of a new environment or in commuting between a nest and familiar feeding grounds e.g. (Merkle & Wehner, 2008; Mittelstaedt & Mittelstaedt, 1980). Species who rely on path integration for foraging typically use global heading information obtained from polarized light or the Earth's magnetic field (Lohmann et al., 1995; v. Frisch, 1949; Wehner, 1997), which reduces error accumulation during path integration (Cheung & Vickerstaff, 2010). As suggested by Nagel et al. (Nagel et al., 2005), humans are also able to use the information of the magnetic north provided by the *feelSpace* belt in a triangle completion task. Expanding the concept of that task, we designed a complex homing task to provide more natural experimental conditions for testing behavioral changes with the *feelSpace* belt. We therefore hypothesize that humans who are provided with the information of the magnetic north via the *feelSpace* belt will be able to use this information in a complex homing task.

Fourth, compatible with the sensorimotor contingency theory that postulates that mastery of new SMCs will be accompanied by changes in the perception of the world (Noë, 2004; O’Regan, 2011; O’Regan & Noe, 2001), we hypothesize to find perceptual changes after the training period with the belt. Using a mixed-method approach of subjective evaluations e.g., (Tashakkori & Teddlie, 2010) we assessed changes in subjective experiences and quantified the extent of changes over the training duration with the *feelSpace* belt. As the belt provides additional navigational information through translating the information of the magnetic north into a tactile signal, we examined both the perception of space in which participants navigate and the perception of the belt’s signal itself. We predict that in the course of training with a sensory augmentation device perception of space as well as of the tactile signal will increasingly be modified.

Consequently, we present a longitudinal investigation involving a seven-week training period with a sensory augmentation device in natural environment as a test several predictions of the SMC theory. In four experiments we explore the hypotheses (H) that learning and mastering the new augmentation signal: (H 1) induces a procedural learning process, (H 2) induces changes in brain activation patterns including the activation of higher motor areas and areas related to navigation, (H 3) will be observable in behavioral changes in a complex homing task, and (H 4) will lead to perceptual changes of space and the tactile belt signal, which are correlated with the training duration. Although, using the sensory augmentation device behavioral results did not reach significance, both EEG and fMRI measurements provided results compatible with the SMC theory and subjects reported significant perceptual changes.

5.3 Results

Participants

Nine participants (19-32 y, *mean* 23.67 y, four females) wearing the *feelSpace* belt all waking hours formed our experimental belt wearing group and five additional participants (21-25 y, *mean* 23.00 y, three females) not wearing a belt formed the control group.

All participants were healthy young adults, without neurologic, psychiatric, or chronic diseases. They were highly motivated and had good introspection and good verbal skills (for details see (Kaspar et al., 2014)). They were selected such that prior to the study they performed plenty of outdoor exercises such as hiking and bicycling. Both groups were asked to continue outdoor activities dedicating them to an unsupervised navigational training during the seven week training period for at least 1.5 h/d in natural environment. Belt wearing participants were asked to explore the belt signal during their navigation activities, while control participants were asked to observe how they navigated during their navigation activities. Both groups were asked to pay attention to their space perception while moving in natural environment.

To ensure that dedicated outdoor navigation (from now on called “training”) and motivation were similar in both groups, belt wearing and control participants recorded their daily training duration and scored their weekly training motivation. The training duration with the belt averaged across the training period of 7 weeks was 1.57 h/d (*SD* = 0.17). The control group performed the navigation training without the belt for the same amount of time (1.57 h/d, *SD* = 0.55). Both groups rated their weekly training motivation with and without a belt, respectively, over the whole training duration as very high (grand mean of 3.97 on a 5 point Likert scale; *SD* belt = 0.30, *SD* control = 0.34) (Kaspar et al., 2014). Thus, belt wearing and control participants showed a high training motivation with no differences in motivation and training duration between groups. All participants were extensively briefed in a dedicated meeting and provided informed, written consent before participating.

The feelSpace belt

The augmentation device, which we used in this study, is a further development of the *feelSpace* belt designed by Nagel et al. (Nagel et al., 2005). This belt gives directional information about magnetic north via vibrotactile stimulation around the waist. Here, we developed a special MRI-compatible version of the *feelSpace* belt using non-ferromagnetic piezo-ceramic actuators to study the neural correlates of SMC learning (Fig 1A). An accompanying set of novel portable *feelSpace* belts uses the identical piezo-ceramic actuators and ensures that vibrotactile stimulation is identical in the scanner and in everyday training with the belts (Fig 1B, C). Portable belts in addition contain a control unit, an electronic compass and battery packs to function independently and to allow free movement while wearing the belt (see method section for more details).

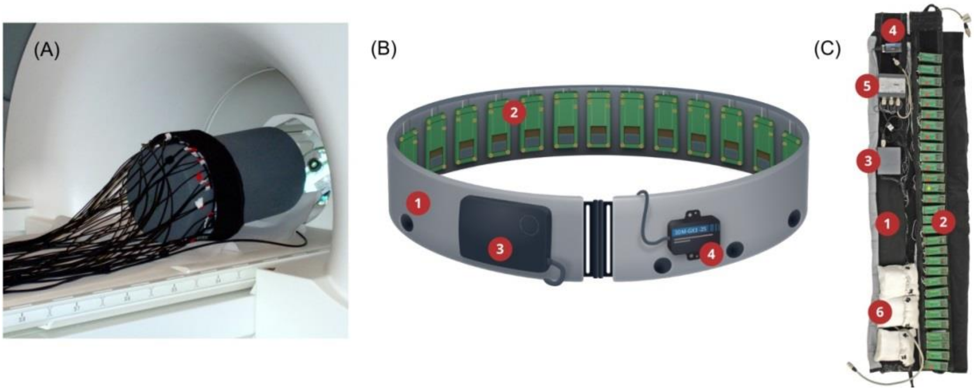

Fig 1. The sensory augmentation device. (A) For testing and demonstration purposes the MRI *feelSpace* belt in the scanner is wrapped around a dummy with cables connecting the vibrating piezo actuators to an external computer. (B, C) The portable *feelSpace* belt (1) consists of the following main components: 30 vibrotactile piezo actuators that are identical to those of the MRI compatible belt (2), compass-control unit (3), an electronic compass (4), piezo-control unit with identical control as the scanner unit (5), and battery packs (6). Figure A taken from Keyser (Keyser, 2010) and under Creative Commons CC-BY-3 from Schumann (Schumann, 2012).

Study design

Before the start of the training period, we conducted baseline measurements for all participants recording sleep EEG, fMRI, and a behavioral homing task and performed specifically designed and standardized questionnaires as well as interviews (Kaspar et al., 2014). At this time point both groups revealed comparable results (see in detail in the separate result sections). The sequence of these measurements was chosen according to the availability of the fMRI and sleep EEG labs. The same measurements were performed at the end of the seven-week training period (see Table 1). We chose seven weeks for our training period as a trade of between reasonable burden for the participants and a time period sufficient for the induction of observable effects (Kärcher et al., 2012; Kaspar et al., 2014; Nagel et al., 2005; Schumann, 2012). In addition to the experiments proper and to the self-guided everyday navigation training, all participants took part in a supervised weekly outdoor training. The outdoor trainings had a large scope from angle turning training to a “treasure hunt” in a natural environment. The study was performed in four cohorts each lasting for eight to nine weeks with a seven-week training period. Our study complied with Helsinki Declaration guidelines and was approved by the ethics committee of the University Osnabrück.

Before Training	**Main Training Period**	**Last Week of Training**
Sleep EEG	Sleep EEG (night 1 and 4)	Sleep EEG
fMRI		fMRI
Homing		Homing
Questionnaires	Daily and weekly Questionnaires	Questionnaires
Interview	Weekly Interview	Final Interview

Table 1. Timetable of measurements.

Hypothesis 1: Training with the feelSpace belt involves procedural learning, observable in neuronal signatures of sleep.

According to previous studies, learning-dependent changes are reflected in general sleep architecture and tonic EEG activity (Fogel et al., 2007; McGaugh, 2000; C Smith, 1995). Specifically, procedural learning induces an increase of REM sleep duration and changes of power in the sigma frequency range during stage 2 sleep and slow-wave sleep. Thus, we performed sleep EEG measurements and recorded four nights per participant. Belt-induced learning was expected to be most prominent in the early training phase. Therefore, we recorded a baseline night before the start of the study, two additional nights at the beginning of the training period (first and fourth night), and one night in the last week of the training period. We excluded one participant from the analyses due to poor sleep quality (i.e. more than 20% of awake and 20% of stage 1 sleep in the EEG data throughout the baseline measurement and the first test night). Four independent coders rated the sleep EEG data following the standard sleep scoring criteria with an inter-rater reliability of above 90% (Iber, Ancoli-israel, Ph, Chesson, & Quan, 2007).

The sleep parameters showed a skewed distribution, and we used a one-tailed permutation test with 10^5 samples for the analysis. The baseline measurement showed no significant differences in sleep stage durations between the belt wearing and the control group (belt vs. control REM sleep duration difference $p = 0.46$, for all other sleep stage durations p values range from 0.29 to 0.46). Further results revealed changes in sleep architecture in the belt wearing group after onset of the belt training (Fig 2A and B). In particular, we found a significant increase of REM sleep duration in the belt wearing group ($p = 0.037$) in the first night after training onset compared to the baseline night. This increase of REM sleep returned to the baseline level towards the end of the training period. Additionally, we found a decrease of stage 1 sleep in the first night of the training period compared to the baseline measurement ($p = 0.037$). In contrast to the belt wearing participants, control participants showed an increase of REM sleep duration towards the end of the training duration, which did not reach significance (p values ranging from 0.119 (baseline - last night) to 0.412). Furthermore, control participants showed no significant changes in stage 1 sleep (p values range from 0.117 to 0.41) and we observed for both groups (for belt group: p values range from 0.256 to 0.454 and for control participants: p values range from 0.110 to 0.345) no significant changes for Non REM sleep parameters (stage 2).

To further analyze learning-dependent changes relative to the baseline night in the EEG spectrum, we focused our power spectrum analysis on three frequencies (delta: 0.5-4 Hz, theta: 4-8 Hz, sigma: 12-16 Hz) that are representative of SWS, REM, and stage 2 sleep phases, respectively. Comparing to the baseline data we performed a separate spectral EEG analysis computing a 2 x 3 x 2 (group x night vs. baseline x electrode placement) mixed-measures ANOVA. For the electrode placement we concentrated on frontal and central electrode placement (Werth, Achermann, Dijk, & Borbély, 1997; Zeitlhofer et al., 1993). For the baseline night we compared the belt wearing group and the control group with an independent t-test, which revealed no significant differences between groups before the training (delta power: $t(11) = -1.473$, $p = 0.169$, theta power: $t(11) = 0.195$, $p = 0.849$, sigma power: $t(11) = 0.761$, $p = 0.462$). For the delta and theta frequency bands the ANOVA revealed no significant main effects for group, night or electrode placement (all $F \leq 3.129$, $p \geq 0.105$), nor significant interactions (all $F \leq 1.451$, $p \geq 0.254$). However, in the sigma frequency band we found a significant between-group effect ($F(1, 11) = 5.358$, $p = 0.041$) and a significant within-group effect for nights ($F(2, 22) = 7.878$, $p = 0.003$). A follow-up analysis using paired t-tests revealed a significant decrease in sigma power from the baseline to first night of the belt wearing group ($t(7) = 5.587$, $p = 0.001$), (Fig 2C and D). Towards the end of the training, sigma power values returned to their baseline levels reflected in the means (mean baseline = 0.4204, mean last night = 0.4239) and in a significant increase from the first night to the last night ($t(7) = -3.792$, $p = 0.007$). For the control group no significant changes in sigma power over nights were observed ($t(4)$ = -0.116, p = 0.913, $t(4)$ = 0.855, p = 0.441 and $t(4)$ = 1.289, p = 0.267, for first, fourth and last night respectively). Due to the small sample size, we also validated all results by using a non-parametric Friedman-test suitable for small sample size analyses. All results could be replicated.

Summarizing, the sleep EEG measurements revealed in the belt wearing group a significantly increased REM sleep duration indicative of procedural learning and significant EEG sigma power decrease indicative of sensorimotor processing early in the training period.

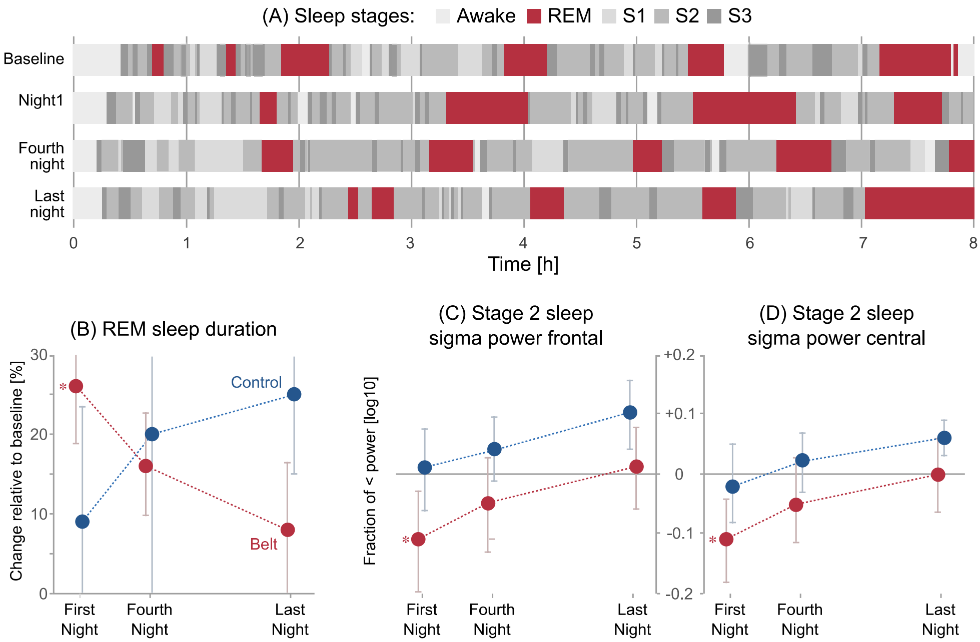

Fig 2. Single participant and group statistics of sleep EEG. (A) Hypnograms of a belt wearing participant demonstrating the distribution of sleep stages during the nights (abscissa) before and during training (top to bottom). REM sleep phases are marked in red. (B) Relative changes in the REM sleep duration for all belt wearing participants and controls during the training period. (C, D) Learning-dependent changes in the sigma power (12 – 16 Hz) during Stage 2 sleep at frontal (C) and central (D) electrodes in belt participants and in controls. Error bars depict SEM. Please note that SEM is influenced by variance as well as group size. An asterix indicates a significant effect.

Hypothesis 2: Training with the feelSpace belt induces changes in cortical activation, in particular in motor centers and brain regions involved in navigation.

We investigate the physiological basis of sensory augmentation via fMRI measurements. During the recordings the participants viewed a minimalistic virtual environment from a first-person perspective on a monitor. Participants performed a virtual *homing* task, and a *control task* with identical visual and tactile stimuli (adapted from (T. Wolbers, Wiener, Mallot, & Buchel, 2007)). All participants were wearing the fMRI compatible version of the belt during the recordings. In half of the trials of either task the belt was switched on coherently indicating participants' virtual direction towards an arbitrarily but consistently defined virtual north via vibration. In the other half of all trials the belt was switched off to measure path integration abilities in the absence of the belt information. This resulted in a four factor (2 x 2 x 2 x 2) design: *belt* (on/off), *task* (homing/control), *group* (belt wearing/control group), and *date* (before/after training). Here, we concentrate on the four main effects and the significant two-way interactions.

For the analysis we used a mixed-effects ANOVA to decompose the four factors and report the main effects of BOLD activation and two-way interactions. We defined regions of interest (ROIs) to concentrate on areas relevant for sensorimotor processing and spatial navigation including higher-level regions. We chose the ROIs considering areas previously defined in similar studies (e.g. (Bremmer et al., 2001; Dukelow et al., 2001; H. O. Karnath, Berger, Küker, & Rorden, 2004; T. Wolbers et al., 2007)). The ROIs were analyzed, and results are reported for clusters larger than 5 voxels when the activation difference was significant with $p < 0.05$ (FDR corrected). Table 2 gives an overview of ROIs and significant activations. Figure 3 shows the canonical MNI T1 weighted anatomical image as a backdrop. Superimposed on the structural scans are the activation differences in the ROIs with $p < 0.001$ (uncorrected). Coordinates are given in MNI space and definitions and labeling of the ROIs were mainly taken from the Anatomical Automatic Labeling atlas from the Wake Forest University Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) and the anatomy toolbox of SPM (Eickhoff et al., 2005). In the figures, we show the planes where the highest number of ROIs and significant activation differences are visible. Thereby, peak activation differences of single ROIs may lie in adjacent planes. All figures show the three planes in z, y, x-coordinates of MNI-space.

The main effect *belt* (Fig 3A) compares brain activation between the condition where the tactile belt is switched on versus the condition where the belt is switched off. Investigating the main effect *belt*, we observe in the *on* condition a significantly higher bilateral activation as in the off condition in the primary somatosensory cortex (S1) and secondary somatosensory cortex (S2) as well as the insula, superior temporal gyrus (STG), and the right posterior parietal cortex (PPC). Thus, we see significant activation of somatosensory regions when the tactile signal of the belt is given. The main effect *date* (Fig 3B) contrasts the activation difference between the pre- and post-training date. The main effect *date* shows a differential activation of the premotor cortex and the supplementary motor area (SMA). Specifically, after the training period the BOLD signal in motor areas is reduced. The effect date reveals an activation difference between before and after training in higher order motor areas. The main effect *task* (Fig 3C) compares the brain activation differences between the virtual homing task and the control task. In this main effect we found a significant activation difference in a large sensorimotor network, including S1, the PPC, medial superior temporal cortices (MST), the insula, the premotor area, SMA, and the cerebellum. Additionally, the differential activation uncovers a higher activation for the homing task in the caudate nucleus. We found differential activation of a large sensorimotor network and of areas that are known to be involved in navigational aspects. The main effect *group* (Fig 3D) compares the activation differences between the belt wearing and the control group. On average, the control participants show higher activation of the hippocampus than the belt wearing participants. The main effect of *group* shows a difference in right hippocampus activation between the two groups. The evaluation of the two-way interactions revealed significant activation differences in the interactions of *date*belt* and *date*task*. The remaining interactions (group*date, group*belt, group*task and belt*task) did not show significant activation differences in the predefined ROIs. The interaction of *date*belt* (Fig 3E) compares activation differences of *belt* signal *on* and *off* contingent on the time of recording before or after the training. Significant activation differences in the interaction *date*belt* were observed in regions S2, PPC, MST, and the insula. Specifically, the activation of S2 revealed significant differences in the *belt on > off* condition only in the first measurement before the training period. After the training period there is no significant activation difference between the *belt on* and *belt off* condition in S2. We found a reduction of belt on/off activation differences after the training especially in the secondary somatosensory cortex.

The interaction *date*task* (Fig 3F) compares activation differences in the *homing* and *control* task before and after training with the *feelSpace* belt. In this interaction we found significant differential activation in the cerebellum and the caudate nucleus. In the cerebellum, before the training period the *homing* and the *control* task revealed no significant activation differences. However, after the training we observe a significantly higher activation in the *homing* than in the *control* task. In the caudate nucleus we found no activation difference before and after training in the *control* task compared to the homing task, which reveals a higher activation in the caudate nucleus before compared to after training. These data reveal a time dependent activation pattern difference in the cerebellum and caudate nucleus for the homing and the control task.

In summary, the fMRI measurements indicate that sensory augmentation by means of training with the *feelSpace* belt involves differential activation patterns including sensory areas (S1, S2), higher motor centers (premotor cortex, SMA, PPC, STG, Insula), cerebellum, and brain areas known to be involved in navigation (hippocampus, caudate nucleus).

	Factors					
ROIs	**Belt**	**Task**	**Date**	**Group**	**Date*belt**	**Date*task**
S1	x	x	--	--	--	--
S2	x	--	--	--	x	--
PPC	x(r)	x	--	--	x	--
MST	--	x	--	--	x	--
STG	x	--	--	--	--	--
Insula	x	x	--	--	x	--
Hippocampus	--	--	--	x	--	--
Premotor cortex	--	x	x	--	--	--
SMA	--	x	x	--	--	--
Primary	--	--	--	--	--	--

<table>
<tr><td>motor cortex</td><td colspan="3"></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>Cerebellum</td><td colspan="3">--</td><td>x</td><td>--</td><td>--</td><td>--</td><td>x</td></tr>
<tr><td>Caudate</td><td>--</td><td>x</td><td>--</td><td>--</td><td colspan="2">--</td><td colspan="2">x</td></tr>
</table>

Table 2. Table of defined ROIS and overview of activations (x= significant activation with p <= 0.05 (FDR corrected), - = no significant activation, r = right)

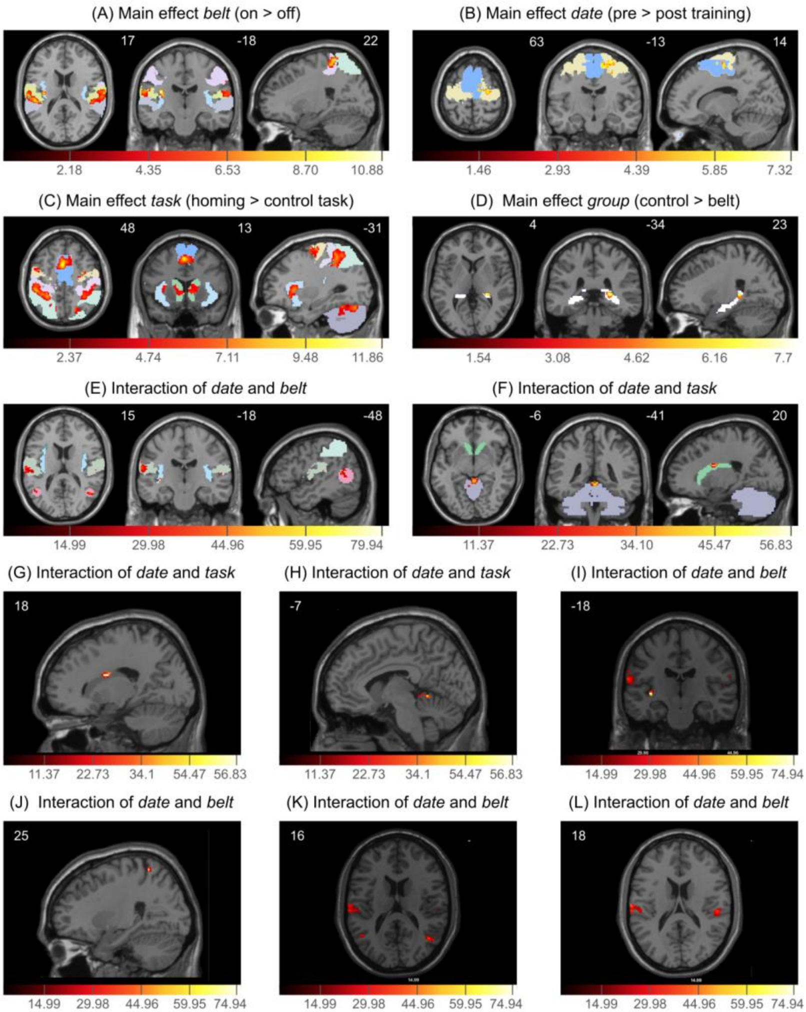

Fig 3. Main effect and 2-way interactions in the fMRI data. Significant BOLD activation differences (the activation color-coding is depicted below the figures) in ROIs in z-, y-, x-planes (coordinates are depicted on top of each panel). (A) Main effect belt (on > off), (B) Main effect date (pre > post training), (C) Main effect

task (homing > control task), (D) Main effect group (control > belt), (E) Interaction of date and belt, (F) Interaction of date and task. Captions color-coding ROIs in Fig 3(A)-(F): S1, S2, PPC, STG, Insula, premotor cortex, SMA, cerebellum, caudate nucleus, Hippocampus, MST. (G-L) Blown ups of planes best depicting peak activations in ROIS of significant BOLD activation differences in two-way interactions: (G) Interaction date x task, peak activation of caudate nucleus, (H) Interaction date x task, peak activation of Cerebellum, (I) Interaction date x belt, peak activation of insula, (J) Interaction date x belt, peak activation of PPC, (K) Interaction date x belt, peak activation of MST, (L) Interaction date x belt, peak activation of S2, (S2 also depicted in I and K).

Hypothesis 3: After training with the feelSpace belt participants successfully utilize the belt in a complex homing task.

To investigate behavioral changes with the belt we designed a homing paradigm as an extension of the conventional triangle completion task. It consisted of eight carefully crafted, complex, curvy polygons without intersections (Fig 4A). The design of the figures was supposed to trigger continuous updating (for more detail see method section). While solving the homing task, participants additionally had to memorize numbers as a cognitive load.

Our main variable was the distance between starting point (Fig 4B, S) and the point where the participant finished homing (Fig 4B, red dot)), the so-called homing error. A separate analysis of the angular error led to identical results. For the analysis we rotated polygons and mirror reversed them as necessary to align the optimal homing trajectories (Fig 4A; black dashed line from H to S with the polygon below). To investigate comparability between groups at the beginning of the training period we performed an independent t test for the baseline measurement date before the start of the training. We found no significant difference between the belt wearing and control group ($F = 2.901$, $p = 0.114$) at this time point. To evaluate the effect of the belt information on the navigation performance, we visualized the difference of homing error in the belt-off minus the belt-on condition for both groups before and after the training period (Fig 4D). Our data show a decrease in performance in the pre-measurement when the belt information was given in both groups, hypothetical because of the additional unknown sensory input. This effect of the belt signal is reversed after training only in the belt wearing group.

For statistical evaluation of navigational performance we performed a 2 x 2 x 2 (*date*, *belt*, and *group*) mixed-measures ANOVA. However, the results revealed no significant main effects of *group* ($F(1,12) = 3.425$, $p = 0.089$), *date* ($F(1,12) = 3.066$, $p = 0.105$), or *belt* ($F(1,12) = 1.446$, $p = 0.252$), nor for interactions ($F(1,12)$ between 0.298 and 1.217, p values between 0.595 and 0.292). Summarizing, our results showed no significant change in performance neither for belt wearing nor control group.

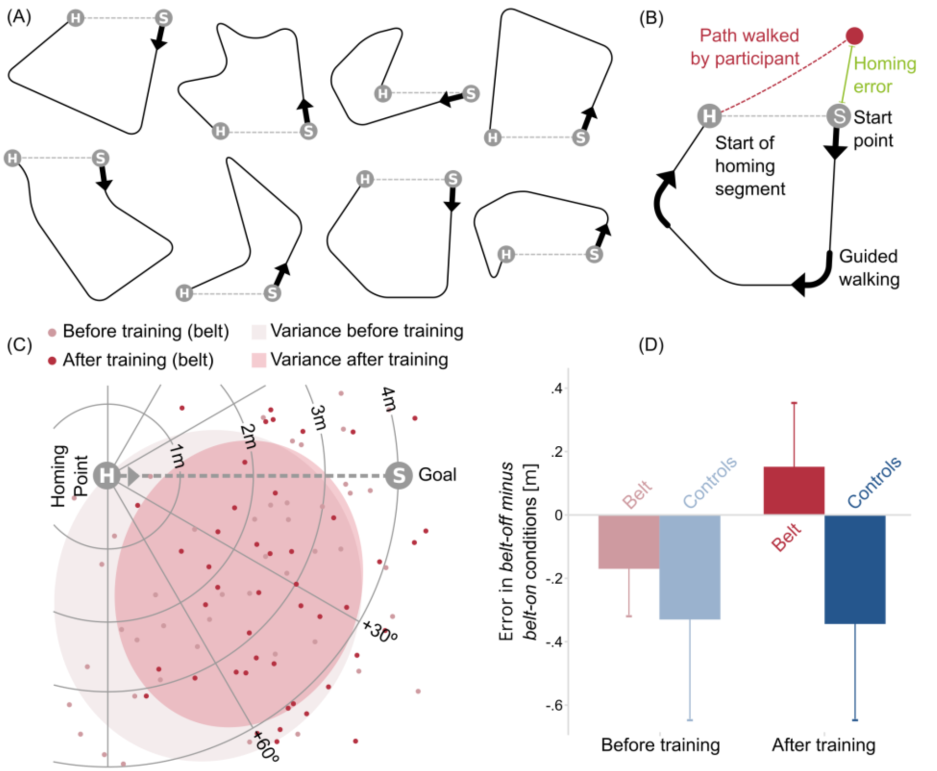

Fig 4. Layout of the homing task. (A) Design of the polygons used in the homing task. (B) Example polygon depicting the homing error (error between start point and actual end point of participants walk), H= Homing point, point from which participants had to home to the starting point on their own, S= Start point, red dot = actual end point of participants' path, grey dashed line H-S = ideal homing segment. (C) Pre- to post-training comparison of homing errors of belt wearing participants in the *belt-on* condition. For visualization polygons were superimposed and mirrored and/or rotated in a way that all of them end up below the dashed line

which represents the optimal path from homing point (H) to starting point (S). An inward error could be observed in the position of the ellipse underneath the homing trajectory could be observed. (D) Effect of belt use (error in *belt-off minus belt-on* conditions, positive numbers indicate a reduction of homing error) onto homing error comparing pre- to post-measurement for belt wearing and control group. Error bars indicate SEM.

Hypothesis 4: Learning of new SMCs with sensory augmentation leads to perceptual changes that are positively correlated with training duration.

To assess subjective perception we developed daily and weekly questionnaires with supplementary weekly interviews for in-depth evaluation of participants' experiences. To obtain qualitative and quantitative estimations of changes questionnaires contained open-ended questions and 5-point Likert items ("not agree" (1), "a little agree" (2), "more or less agree" (3), "quite agree" (4), to "very agree" (5) or "never" (1), "seldom" (2), "sometimes" (3), "often" (4), to "always" (5)). In the questionnaires of the control participants' questions were phrased in close analogy to the belt questionnaire substituting "with the belt" by "since I train my orientation" in questions not referring to the belt signal experience as such. Apart from this, we kept the phrasing of the questions equal. Special items referring to the belt signal experience had to be excluded in the control questionnaire, naturally (for more details see the method section below).

Additionally, we evaluated the German version of the NEO-FFI (Borkenau, P. & Ostendorf, 1993) and the ACS-90 (Kuhl, 1994) to asses relevant personality traits and the "Fragebogen Räumliche Strategien" (FRS) (Münzer & Hölscher, 2011) to asses navigational behavior. Participant groups did not significantly differ in personality traits (Mann-Whitney-U-test for NEO-FFI: all $Z = -1.67$ or smaller, all $p = 0.11$ or bigger and for ACS-90: all $Z = -1.17$ or smaller, all $p = 0.30$ or bigger). In the FRS for the baseline measurements groups also did not significantly differ (Mann-Whitney-U-test all $Z = -0.67$ or smaller, all $p = 0.52$ or bigger). For the belt wearing group we measured the AttrakDiff2 (Hassenzahl, Burmester, & Koller, 2003) questionnaire to assess the *feelSpace* belt. These latter questionnaires and the qualitative data of our daily and weekly questionnaires have been thoroughly analyzed and published elsewhere (Kaspar et al., 2014).

	Loading on Factors				
Questions defining the items	**#1**	**#2**	**#3**	**#4**	**r^2**
With the belt I can give more precise estimations on how streets are related to one another.	0.88	-0.28	0.00	0.07	0.86
With the belt it is easier for me to indicate the position of different places to each other.	0.84	0.33	0.22	0.19	0.90
With the belt I am always aware where I am located in relation to my home.	0.70	-0.43	0.40	-0.11	0.85
Since wearing the belt I am more aware of the cardinal directions.	0.65	0.28	-0.05	-0.41	0.67
I have the feeling that my spatial sense of orientation improved since wearing the belt.	0.26	0.93	-0.03	-0.09	0.95
With the belt I feel safer in a new environment than without the belt.	-0.26	0.87	0.10	0.09	0.85
With the belt it is easier for me to orient myself in a new environment than without the belt.	-0.09	0.74	-0.21	-0.05	0.61
When I take the belt off my spatial sense of orientation decreases.	0.24	0.66	0.10	-0.60	0.85
I do not perceive the transmitted information of the belt as vibration but as something different.	-0.08	-0.15	0.91	-0.27	0.93
I perceive the transmitted information as vibration.	0.25	0.36	0.87	0.16	0.97
After taking the belt off I still perceive a feeling of vibration.	0.17	-0.22	0.83	0.28	0.84
I consciously concentrate on the belt to use its information.	0.03	-0.28	0.03	0.87	0.85
I am always consciously aware of the belt while wearing it.	0.04	0.39	0.09	0.78	0.77
Explained variance [%]	20.76	26.86	19.55	16.58	83.75

Table 3. Factor analysis of quantitative data of the weekly questionnaire for the belt wearing group. The last column (**r2**) gives the communality of the factor loading for each item.

For the analysis of our quantitative data we performed a factor analysis of the Likert items of the weekly questionnaire to evaluate underlying factors. For the factor analysis, we used the Guttman-Kaiser Criterion for factor extraction (factors with eigenvalues larger than 1 were extracted) and used a varimax rotation to rotate the factor matrix. As an item analysis, we calculated mean, variance, and selectivity as well as the item-total correlation for all items. Based on these analyses, no item had to be excluded for the following factor analysis.

The factor analysis of quantitative items resulted in four factors for the belt wearing group. The factor loadings were evenly distributed across these four factors and they jointly explained a major fraction of the variance (see Table 3). Furthermore, the communalities of the individual items ranged between 0.61 and 0.97, resulting in an average of 0.84. The internal consistencies of items (Cronbach alpha) were between 0.62 and 0.85, with an average of 0.79 for the factors of the belt wearing group and 0.67 for the factor of the control group. The item “Since wearing the belt I am more aware of the cardinal directions.” was removed in the statistic from the factor “*space perception*” to allow comparability between the belt wearing and control groups (see below). We choose the labels for the factors due to the common topics of the respective questions of the questionnaire: *space perception* (#1), *trust in navigational ability* (#2), *tactile belt perception* (#3), and *conscious belt perception* (#4). For the control group the factor analysis added up to one factor only. This factor had the largest overlap with the factor *space perception* of the belt group. Therefore we took the intersection and considered only the joint items in the following. The factor analysis revealed a good mapping of our 13 items onto four factors for the belt wearing group (see Table 3) and onto one factor for the control group where we only considered the 3 corresponding items matching the factor *space perception* of the belt wearing group.

For comparability we give here the corresponding item phrasing of the three items loading on the factor “space perception” for the control group: 1. “Since I train my orientation I can give more precise estimations on how streets are related to one another.” 2. “Since I train my orientation it is easier for me to indicate the position of different places to each other.” 3.” I am always aware where I am located in relation to my home. “. To give an insight into the precise reports by the participants, we give here examples of citations for the main categories of the qualitative content analysis (Kaspar et al., 2014) of belt wearing participants (BWP) and control participants (CP).

The following citations give evidence of a profound change of *space perception*. "*Each place in space has now, depending on how I am located to it, an additional information, which I can't yet connect globally*" (BWP 1, week 1). "*Space is getting wider and deeper. Through the presence of objects/landmarks that are not visible my space perception is extending beyond the borders of what I see*" (BWP3, week 6). "*The direction is one information more that is always available. This direction information is no specification of other signals (visual or mental maps), but is really independent thereof*" (BWP 9, week 6).

The increased *trust in navigational abilities* is indicated for example by a participant who stated, *"Because of the permanent knowledge of the northern direction a new space perception develops, a feeling of security"* (BWP 4, week 6).

The *tactile belt perception* is related to space, "*I perceive* [the vibration of the belt] *as an existent information about the northern cardinal direction*" (BWP 4, week 4). *"I perceive the information of the belt as a pointer towards the north direction or a pointer towards places, e.g., the university or my desk at home"* (BWP 8, week 2).

The *conscious belt perception* is clearly changing over time. *"I have the feeling that I don't use the belts information consciously not only in known areas any more, but that I use and feel the signal consciously when I need it. And I need it (…) when I have to orientate myself"* (BWP 8, week 5). "*Once again I noticed that I just use it* [the belt signal] *without being aware of it*" (BWP 7, week 6).

In contrast, statements by control participants give evidence that they have to concentrate for navigation, "*My mental map didn't change a lot. But I am more aware of it*"(CP 5, week 4). "*If I concentrate a lot I can integrate* *other things, e.g., cardinal directions into my space perception. But without deliberately doing this nothing changes*" [German original: aber ohne das bewusst zu machen ändert sich nichts.] (CP 2, week 5).

Thus, the statements of the participants given in the interviews or diaries fully support the factor analysis of the quantitative questionnaires.

Following the factor analysis, we investigated the changes of the ratings for the four factors as a function of the training duration for the belt wearing group (Fig 5). In order to test whether ratings for the factors *conscious belt perception*, *belt information*, *trust in navigational ability* and *space perception* increase over time, we fitted separate linear mixed models for each factor with the continuous predictor weeks. To account for the dependence between measurements within individual participants, we modeled individual intercepts for each participant (Twisk, 2006). We found that all models yielded significant positive slopes, indicating an increase in ratings over time (Fig 5). The highest increase in ratings is found for the factor *tactile belt perception* (B = 0.24, p < 0.001, 95% CI [0.18, 0.30]), followed by the factors *conscious belt perception* (B = 0.16, p = 0.001, 95% CI [0.10, 0.21]), *trust in navigational ability* (B = 0.13, p = 0.017, 95% CI [0.07, 0.18]), and *space perception* (B = 0.11, p = 0.002, 95% CI [0.07, 0.15]). Using for this factor the same items for the belt wearing group as for the control group did not change the result (B = 0.11, p = 0.003, 95% CI [0.05, 0.17]). When we performed the same analysis for the factor of *space perception* in the control group, we did not find a significant slope (B = 0.007, p = 0.90, 95% CI [-0.12, 0.14]), indicating that participants' *space perception* ratings in the control group did not increase over time. In the belt wearing group, factor ratings for all four factors increased significantly over time whereas in the control group ratings for the (only) factor *space perception* did not change over time.

In addition, we investigated the difference in ratings for the factor of *space perception* between the belt wearing and the control group over the training duration (Fig 5). To investigate comparability between groups at the beginning of the training period we performed an independent t test for the first measurement date after one week of training. We found no significant difference between the belt wearing and control group (F = 0.071, p = 0.794) at this time point. We then compared whether participants in the belt wearing group showed a steeper increase in *space perception* ratings over weeks in comparison to the control group. For this purpose, we examined how the slopes as a function of weeks differed between the groups using a linear mixed model. We found that the slope is significantly larger for the belt wearing group in comparison to the control group ($B = 0.10$, $p = 0.005$, 95% CI [-0.17, -0.03]). Belt wearing participants' rating increase for the factor *space perception* over weeks was significantly larger than in the control group.

Taken together, we observed a continuous increase of the ratings of all factors (*space perception, trust in navigational ability, tactile belt perception, and conscious belt perception*) over the training duration in the belt wearing group. The longer the belt wearing participants wore the belt the higher they rated all factors indicating a continuous evolution of changes in subjective experiences over time. In contrast, the rating for the factor (*space perception*) in the control group showed no systematic change over time. The comparison of the factor *space perception* between belt wearing and control groups revealed a significantly higher rating increase in the belt wearing group over weeks. Therefore, we can conclude that the training with the *feelSpace* belt led to increasing changes of subjective experiences of perception of space and perception of the belt signal and trust in navigational ability over time.

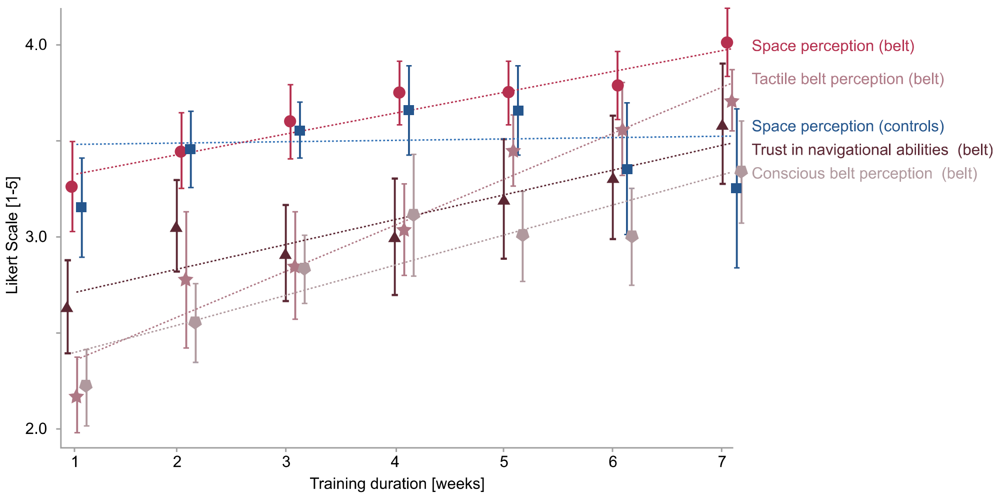

Fig 5. Factor ratings for the belt wearing and control group. Ratings for factors *trust in navigational ability* (black triangles), *tactile belt perception* (pink stars), *conscious belt perception* (light pentagons) and *space perception* (red circles) for the belt wearing group and *space perception* (blue squares) for the control group as a function of weeks. Ratings range from 1 to 5 (not agree to very agree), indicating a low or high rating for the factor, respectively. Dotted lines indicate fitted lines by a linear mixed model for each factor. Error bars are SEM.

5.4 Discussion

In the present study, we experimentally tested several predictions of the SMC theory by observing the learning and mastery of a new sensory signal given with a sensory augmentation device. The increased REM sleep duration in the early training phase with the *feelSpace* belt indicated an intensified procedural learning process (hypothesis 1). The decrease in sigma power only in the belt wearing group at the same time suggested increased sensorimotor processing. FMRI measurements revealed during a virtual homing task a differential activation of sensory and higher motor areas, i.e., PPC, SMA, premotor cortex, and brain areas known to be involved in navigation (hypothesis 2). Furthermore, after seven weeks of training neither the belt wearing nor the control group showed a significant increase in performance during a complex navigation task (hypothesis 3). Evaluation of participants' subjective experiences, while using the belt, indicated a continuous evolution of changes with increasing training duration in the perception of space and of the belt signal, as well as an increasing trust in navigational abilities when using the belt (hypothesis 4). Evaluation of control participants' reports revealed no changes of their spatial perception over time. In summary, our results provide no support for hypothesis 3, but give evidence that the present kind of sensory augmentation leads to procedural learning, involvement of motor areas and areas involved in navigation with concomitant perceptual changes in subjective experiences. Our experimental results comply with predictions of learning new sensorimotor contingencies.

Procedural learning

Our hypothesis that training with the *feelSpace* belt induces procedural learning was supported by sleep-EEG measurements. Here we found a significantly increased fraction of REM sleep duration in participants training with the *feelSpace* belt with a maximum in the first training night whereas control participants showed no significant changes of REM sleep duration over the training period. Previous studies on humans (Maquet, 2001; Walker & Stickgold, 2004) and animals (McGaugh, 2000; Smith, 1995) reported that procedural learning leads to an increased REM sleep duration. Once animals mastered performance of these tasks, REM levels returned to normal (Hennevin, Leconte, & Bloch, 1971; Leconte & Hennevin, 1971). This observation is in line with our results, showing that REM sleep duration in belt wearing participants returned to the level of the baseline night by the end of the seven weeks training period. Taken together, the changes of REM sleep duration suggest that training with the *feelSpace* belt induces a procedural learning process.

To further investigate the procedural learning process we also evaluated tonic EEG activity during sleep. Fogel et al. (Fogel et al., 2007) reported an increase of sigma power during Stage 2 sleep and slow wave sleep following periods of procedural learning. Unexpectedly, we found a significant decrease in sigma power (12 – 16 Hz) in frontal and central electrodes during Stage 2 sleep following training onset with the belt whereas control participants showed no significant changes in the power analysis. In line with our result, however, Campus et al. (Campus et al., 2012) observed a similar effect in an experiment on sensory substitution involving supramodal mental mapping both in blind and sighted subjects. They specifically explored the lower beta frequency band, due to its role in short-term memory (Tallon-Baudry, Bertrand, & Fischer, 2001) and complex associative functions (Weiss & Rappelsberger, 1996). In their study in both blind and sighted subjects, low beta power decreased after active exploration of a virtual environment with a sensory substitution device. This decrease was suggested to be associated with motor programming (Campus et al., 2012). Additionally, the power decrease after active exploration of the environment was proposed to be caused by increased sensorimotor processing after tactile stimulation (Neuper, Wörtz, & Pfurtscheller, 2006; Perfetti et al., 2011). Therefore, the observed decrease in sigma power during sleep in the present experiment might indicate increased sensorimotor processing and motor programming in the early training with the *feelSpace* belt.

Training and involvement of cortical areas

The fMRI measurements during virtual navigation showed that training with the *feelSpace* belt influences activation of sensory and higher motor brain regions. We observed a differential activation in the primary and secondary somatosensory cortex and the insula, structures known to be involved in sensory processing (Burton, Videen, & Raichle, 1993; Dijkerman & De Haan, 2007; Johansen-Berg, Christensen, Woolrich, & Matthews, 2000; Maldjian et al., 1999). Additionally, we found a significant activation difference in the superior temporal gyrus (STG) and in the right posterior parietal cortex (PPC). In the navigation and control condition participants received tactile belt information and visual cues in the form of optic flow to solve the task. However, they lacked other sensory information like vestibular or kinesthetic information. Therefore, we assume that the activation of early sensory areas reflects the processing of the tactile belt signal. The STG is known to be a polysensory spatial area in which multimodal sensory input converges into higher order spatial representations (Karnath, 2005). We hypothesize therefore, that the finding of an activation of the STG indicates integration of tactile signals provided by the belt and visual information (Wahn & König, 2015a). Additionally, we found an activation of the PPC that contributes to sensory-motor functions and transformations (Creem-Regehr, 2009), somatosensory and motor integration (Culham & Valyear, 2006; Iacoboni, 2006), and spatial attention (Corbetta, Shulman, Miezin, & Petersen, 1995; Wolpert, Goodbody, & Husain, 1998). Taken together, our fMRI results revealed a differential activation of brain areas known to be involved in sensory processing and in sensorimotor integration.

We hypothesized that after a training period that is sufficient to induce observable effects with the *feelSpace* belt also changes in brain activation would be observable. In our experiments, we observed a significant reduction of activation in SMA and premotor cortex after the training period. This is in line with previous work on learning to control a brain-computer interface (Wander & Blakely, 2013) that found a decrease of initially high activation in prefrontal cortex, premotor cortex, and PPC once participants learned to master the brain-computer interface. A decrease of activation in the premotor cortex has also been found as an effect of procedural learning (Kassubek, Schmidtke, Kimmig, Lücking, & Greenlee, 2001), in line with the results obtained by the sleep EEG described above. Furthermore, the two-way interaction comparing the belt signal and the time of measurement (*date*belt*), revealed a change in the activation pattern. These changes were especially marked in S2, where we found a reduction of activation differences after the training period. This suggests that belt training is accompanied by a change of how the belt's signal is processed. In the literature, the effects of training on changes in neural functions are heterogeneous: Practice-related activation changes may result in an increase or a decrease in activation of involved brain areas as well as in a reorganization of activated areas (Grill-Spector, Henson, & Martin, 2006; Kelly & Garavan, 2005). Activation decrease is a common finding in examining task practice. The main mechanism, which is proposed to underlie activation decreases, is an increase in neural efficiency, sometimes called sparsification (Peterson, van Mier, Fiez, Raichle,1998; Poldrack, 2000), which is suggested to be the cognitive consequence of greater skills at applying the initial strategy (Jonides, 2004). A reduction of premotor activity is also compatible with the skilled attention hypothesis (Clark, Schumann, & Mostofsky, 2015), which proposes that the control of attentional processes within a domain becomes an aspect of the skill and less volitional as the procedural repertoire becomes more flexible and robust against distortions, leading to an improved mastery of the domain. Therefore, our finding of a decreased activation in sensory and in higher motor areas after the belt training period might indicate a training induced increase in neural efficiency.

The influence of "navigation" onto cortical activation pattern

As the *feelSpace* belt delivers continuous information about orientation in space, we hypothesized that this would also modulate activity in brain areas known to be involved in navigation. To address this question, the fMRI measurements compared a virtual homing task and a control task in close analogy to the task in Wolbers et al. (Wolbers et al., 2007). In this comparison our results revealed a higher activation in the homing than the control task in a large sensorimotor network including S1, Insula, PPC, MST, premotor cortex, and SMA as well as in the Cerebellum and the caudate nucleus. As known from previous work, MST is involved in extracting heading information from optic flow (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Orban et al., 1995), reflecting the optic flow in the performed homing task. SMA is known to be involved in the control, planning, initiation, and execution of movements (Cunnington, Windischberger, & Moser, 2005; Penfield, 1951; Tanji, 1994). The premotor cortex is mainly involved in sensory predictions and polymodal motion processing (Bremmer et al., 2001), as well as understanding of motor events (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). As the participants did not move in the scanner, the activation of these motor areas presumably reflects the imagined movements in the virtual navigation task. The cerebellum was reported to be involved in predictions about sensory consequences of actions (Blakemore, Frith, & Wolpert, 2001). Furthermore, previous studies found evidence for the involvement of the Cerebellum in navigation (Iglói et al., 2014). It was reported that the caudate nucleus is also involved in navigation (Iaria et al., 2003), especially during route following (Hartley, Maguire, Spiers, & Burgess, 2003) and way finding (Voss, Fortin, Corbo, Pruessner, & Lepore, 2013). In the two-way interaction comparing *date and task* we found significant differential activation in the cerebellum and the caudate nucleus. In the cerebellum, we only observed after the training a significantly higher activation in the *homing* than in the *control* task. The increased cerebellar activation during the homing task could thus be understood as a reflection of the necessity of predicting the sensory outcome of the imagined movements in the virtual environment. In the caudate nucleus we found only in the homing task a higher activation before compared to after training. These results reveal differences in the activation pattern in the cerebellum and caudate nucleus for the homing and the control task depending on before or after the training. Unexpectedly, we found a significant activation difference in the right hippocampus between control and belt wearing participants with a higher activation in the control group. The hippocampus is a region that is often involved in navigation tasks (Iaria et al., 2007; Maguire et al., 1997; Spiers & Maguire, 2006). Hippocampal activation is usually investigated and observed in connection with memory tasks. Specifically, hippocampal activation is found in tasks when memory retrieval is relevant for forming cognitive maps (Iaria et al., 2007; Thomas Wolbers, 2005), navigating successfully in learned environments (Maguire et al., 1998; Maguire et al., 1997), and when tasks include landmarks (Morgan, MacEvoy, Aguirre, & Epstein, 2011). Evaluating qualitative reports of subjective experiences of the seven weeks training period of belt wearing and control participants Kaspar et al. (Kaspar et al., 2014) found that the navigation strategies that were used while navigating in natural environment differed between groups. The belt wearing participants reported to more and more rely on the *feelSpace* belt's information for navigation whereas all control participants reported to use landmarks and most also city maps. Furthermore, belt wearing participants reported that using the belt enabled a more intuitive navigation with less cognitive effort (Kaspar et al., 2014). These differences in navigation strategies reported by the belt wearing and control participants might relate to the differential activation observed in the hippocampus. Also, Wolbers et al. (Wolbers et al., 2007) found right hippocampal activation in a similar task to ours only in correlation with pointing accuracy, which they suggested to show strong engagement to be necessary for accurate updating. Taken together, these data demonstrate the differential activation of cortical areas related to spatial navigation.

Behavioral evaluations

We assessed behavioral changes induced by training with the *feelSpace* belt by measuring participants' performance in a complex homing paradigm. With our task design, in comparison to the classical triangle completion task, we aimed at task conditions that were planned to induce continuous updating of a homing vector against a natural human tendency to solve homing via survey reconstruction (Fujita et al., 1993). To make it harder to solve the homing task by means of cognitive reasoning we additionally added a memory task for increased cognitive load. Here, improvement of homing performance after the training period with the *feelSpace* belt did not reach significance. A number of factors might contribute to this negative result. First, even though Wiener and Mallot (Wiener & Mallot, 2006) demonstrated in a visual speeded point-to-origin task that increasing path complexity does not necessarily negatively influence path integration abilities, path complexity might have an influence on performance in a real world navigation task. This is in line with the predictions of most common path integration models for humans (Fujita et al., 1993). Indeed, a previous study investigating a homing task using the *feelSpace* belt (Nagel et al., 2005) found an improvement of task performance after the training period with less complex polygons. Second, recent research on spatial attention of vision and haptics indicate shared attentional resources (Wahn & König, 2015b) and a task dependence of visuotactile processing (Wahn & König, 2016) but no influence of attentional resources on optimal visuotactile integration. These findings suggest that our dual task design of path integration combined with a number memory task have not limited the integration of tactile signals in this complex task. Third, we have to consider that the spatial dimensions of the homing task were still rather small compared to natural settings. The polygons were of a length of 19-22 m and path completion took less than a minute. This is a scale where signals supplied by the vestibular system are still reliable. Thus, in the absence of belt signals participants might rely on the vestibular information. To address this shortcoming, we designed a large-scale pointing task when studying a congenitally blind subject (Schumann, 2012) that was then also used in a study with a late-blind participant (Kärcher et al., 2012). The results revealed significant performance improvement for the late-blind participant after the training period with the *feelSpace* belt (Kärcher et al., 2012). The results with a congenitally blind subject indicate that performance improvements with the *feelSpace* belt depend on the navigation strategy spontaneously employed by the perceiver, and can be largely enhanced by training a strategy suited for the information of the belt. The evaluation of the large scale pointing study with sighted participants is ongoing. Therefore, in the present study we have to consider that the behavioral task as part of the overall study was not optimized to test for training-induced behavioral changes with the *feelSpace* belt.

Perceptual changes

As perceptual changes are an important aspect of SMC theory we thoroughly evaluated subjective experiences of participants in the course of the seven-week training period. Here, we report changes in perception following the training and the influence of the training duration comparing belt wearing and control participants. In the belt wearing group, we found a significant increase throughout the training period of subjective ratings concerning *space perception, trust in navigational ability, tactile belt perception*, and (the inverted scale of) *conscious belt perception*. This indicates, in line with previous studies investigating sensory substitution (Auvray et al., 2007; Ward & Meijer, 2010), that the longer participants train the more detailed perceptual changes occur. Importantly, the active exploration and training with the sensory augmentation device, as used in our study, to improve the richness of the perceptual changes is supported by previous studies using sensory substitution (Lenay, Canu, & Villon, 1997; Charles Lenay et al., 2003; White, Saunders, Scadden, Bach-Y-Rita, & Collins, 1970). In contrast to belt wearing participants, control participants actively training their orientation did not report systematic changes over the training period. Evaluating the development of a new perception of space using the feelSpace belt Kaspar et al. (Kaspar et al., 2014) found that after seven weeks of training eight out of nine belt wearing participants stated to have developed a new spatial perception. In contrast, no control participant reported the development of a new space perception. Our finding of a quantitative increase of rated perceptual changes over time is supplemented by the qualitative analysis of subjective reports of perceptual changes (Kaspar et al., 2014). The main focus of reported changes in space perception concerned spatial relations between self and cardinal directions, self and objects, between objects, alignment of objects towards cardinal directions as a new feature of the objects, and updating and enlargement of mental maps, which then provided a basis for spatial orientation (Kaspar et al., 2014). Thus, the increase of quantitative perceptual changes over time and qualitative perceptual changes when training with the *feelSpace* belt are compatible with the theory of sensorimotor contingencies.

Considerations on study design

Our experimental design is a first step of a series of increasingly refined tests using sensory augmentation. For example, in the present work we compare belt wearing participants with controls who do not have any directional information and do not wear any belt as such. This comparison was driven by the aim to have a control group that moves equally in natural environment and have the belt as the defined difference. As the SMC theory states the importance of action for developing new SMCs a possible control would also be a passive training condition. In fact, a recent study on integration of kinesthetic and vestibular information by EEG in a virtual reality environment reported significant differences in cortical processing between active and passive conditions (Ehinger et al., 2014). To apply such techniques in the context of sensory augmentation is an important next step.

As we have a very complex and demanding study design including a series of different experiments, we had to find a balance between desirable amount of data and the demand on participants and length of the whole project. This lead to a training duration of seven weeks for which a former study (Nagel et al., 2005) had shown significant perceptual and behavioral changes. Previous studies examining sensory substitution (Auvray et al., 2007; Bermejo et al., 2015; Ward & Meijer, 2010) showed that some perceptual aspects of the substituted stimulus were learned in a very short time whereas a prolonged training with the device developed a more detailed perception. Ward and Meijer (Ward & Meijer, 2010) investigated late blind subjects with an auditory to vision substitution device and even after several years of daily use still observed perceptual changes. In line with this finding our subjective data indicate that the learning process did not asymptote within seven weeks. Thus we hypothesize that a prolonged training duration would lead to more pronounced training effects. Furthermore, the complex study design also influenced the number of participants resulting in small unequal groups. Thus, our results give a first report of effects, which have to be explored in detail with a large-scale study and an even longer training duration.

Out of ethic considerations we performed our study with adult participants. As previous studies showed that the human brain is plastic throughout the life span (Pascual-Leone et al., 2005; Proulx et al., 2014), we hypothesized that training with the sensory augmentation device would lead to observable changes in the brain. One mechanism to induce brain plasticity is crossmodal and sensorimotor activation, which could be observed, e.g., in sighted subjects through visual and haptic object recognition (Amedi, Malach, Hendler, Peled, & Zohary, 2001; Amedi, Jacobson, Hendler, Malach, & Zohary, 2002), in blind subjects in auditory verb-generation (Burton, Snyder, Diamond, & Raichle, 2005), in speech comprehension (Röder, Stock, Bien, Neville, & Rösler, 2002), and in Braille reading experiments (Cohen et al., 1997; Sadato et al., 1996) and in sensorimotor learning (Dayan & Cohen, 2011). Related to the theory of the critical period (Wiesel & Hubel, 1963), where brain plasticity is assumed to be restricted to a crucial time gap in early life, several research groups investigated brain plasticity in blind subjects who were born blind or lost sight early or late in life (Büchel, Price, Frackowiak, & Friston, 1998; Röder, Rösler, & Spence, 2004; Norihiro Sadato, Okada, Honda, & Yonekura, 2002). These groups suggest, in accordance, that there is a difference of compensatory plasticity in congenitally and late blind subjects with a susceptible period seemingly before adolescence (in these studies between 12 and 16 years of age). Therefore, we hypothesize that even though our results suggest procedural learning and changes in brain activation following the training with the feelSpace belt in our adult participants that these changes would be even more marked when training with sensory augmentation before adolescence.

Conclusion

With our study design we introduced a practical possibility to investigate the development of new sensorimotor contingencies by means of sensory augmentation. The measurements were designed to test predictions of SMC theory (O’Regan, 2011; O’Regan & Noe, 2001). Specifically, compatible with a procedural learning process, in the early training phase we found indications for increased sensorimotor processing and motor programming in sleep EEG recordings. Investigating brain activity with fMRI revealed an involvement of a large sensorimotor network and areas that are known to participate in navigation. Perceptual changes increased continuously with training duration, thus supporting the notion of SMCs, which postulates that mastery of sensorimotor contingencies is constitutive of conscious perception (O’Regan, 2011; O’Regan & Noe, 2001). The present study motivates us to further investigate the grounding of conscious perception in the concept of SMCs and the approach of embodied cognition. Our findings using sensory augmentation in a real world environment might also encourage practical use in the field of sensory substitution.

5.5 Materials and Methods

Our study complied with Helsinki Declaration guidelines and was approved by the ethics committee of the University Osnabrück. All participants were extensively briefed in a dedicated meeting and provided informed, written consent before participating.

The feelSpace belt

The *feelSpace* belt, in its first version designed by Nagel et al. (Nagel et al., 2005), is a sensory augmentation device that supplies information about magnetic north as vibrotactile information around the waist. For this, a belt was equipped with an electronic compass, a set of 13 vibrotactile actuators, battery packs, and a control unit that always activates the actuator pointing north. Specifically, only the one northernmost element is vibrating, as participants feel irritated when more than one vibration element is active (Nagel et al., 2005).

Here, we developed a special non-magnetic variant of the *feelSpace* belt for use in magnetic-resonance (MR) environments using piezo-ceramic actuators. As we are interested in isolating neural activity selectively related to the directional information conveyed in the tactile signal, it is essential to keep the vibrotactile signal proper identical between daily training and fMRI-testing situations. We therefore also developed a set of portable piezo-ceramic *feelSpace* belts for everyday use during the training. These portable belts accompany the MRI compatible version and utilize the same piezo-ceramic actuators and piezo-driving signals. Hence, our study on sensory augmentation provides the identical tactile stimulation in training and in all tests, including fMRI measurements (Keyser, 2010; Schumann, 2012).

Both belt variants are made of a modular core unit that entails 30 non-magnetic piezo-ceramic bending actuators as vibration devices (PL140.10, Physikinstrumente GmbH & Co. KG, Karlsruhe, Germany). Thus, we more than doubled the spatial resolution of the original belt. Piezo-ceramic actuators are MR compatible (Gassert et al., 2006; Tse et al., 2009) and have been used previously in fMRI experiments (Francis et al., 2000). To provide physical stability for the highly fragile ceramics, and a means of fixation to the belt, each actuator is placed in a custom-made housing build from resistant PCB material that covers most of the actuator and absorbs moderate shocks. A small plastic plate glued at one end of the piezo ceramics provides the surface contact of the vibrotactile stimulation to the skin (Fig 6A). For further insulation, piezo-ceramics and electrical contacts are individually covered with an acrylic thin film coating that also provides water-resistance. Each actuator housing is mounted individually to the belt via a Velcro strip so that the actuators can be distributed evenly for varying sizes of the belt.

In addition to MRI compatibility, our re-design of the *feelSpace* belt entails a number of further improvements over the original version. Electro-magnetic actuators used in the previous belt have a high-latency onset of activation of typically 200ms, while piezo actuators used here achieve a fast activation onset below 10ms. This allows an almost instantaneous change of the tactile signal without noticeable response latencies. Both control logic and compass were selected to utilize this high speed. Thus, our piezo actuators operate at a time scale that is close to other sensory information such as vestibular signals, proprioception or vision (Angelaki & Cullen, 2008). Second, piezo-ceramic actuators allow a precise design of the tactile vibration signal. Vibration frequency was set to about 178 Hz as an optimal sensitivity to tactile vibrations is achieved at frequencies between 150 and 300 Hz (Jones & Sarter, 2008). Lastly, we drastically increased the number of actuators to a total of 30. The placement of the actuators now is fine-graded relative to the discrimination thresholds of skin surface around the waist (Cholewiak, Brill, & Schwab, 2004), and the refined angular resolution of the novel belts requires only a small turn of 12° degree for switching to an adjacent actuator and change in sensation. Hence, the piezo-ceramic belts provide a smooth and low-latency sensation of a counter-rotational movement when turning around the longitudinal body axis with the belt.

To prevent electromagnetic disturbances, in the MRI-compatible version of the belt each actuator is interfaced individually by a shielded coaxial cable of 5 m length connected to the control electronics via low-pass filters and high quality LEMO connectors. The control electronics is kept at a maximum distance to the scanner coil and electrically isolated from the stimulus computer in the experimentation room by an optical cable. For hardware shielding a 30-channel filter-chain system is contained in three separate fully closed aluminum boxes of 10 filters each, which are placed together with an optical control board, a modular generator for the piezo-driving signal, and six 0.8 Ah sealed lead-acid batteries in a further enclosing aluminum case. The modular piezo-driving generator uses a dedicated microprocessor to generate a 178 Hz square wave signal that switches the 22 V DC supplied by lead acid batteries as the piezo-driving signal. The driving signal in turn is directed to an individual piezo bender via optical relays, which also provide optical isolation between actuator and power supply. For electrical shielding, each piezo actuator channel is filtered with 60 dB low-pass filters at 120 MHz, the approximate resonance frequency of protons in a magnetic field at 3 T. The filters connect the piezo ground to the enclosing aluminum case, which is in turn connected with low-impedance to the Faraday cage of the scanning room to dissipate any high-frequency energy that might have been induced. Dedicated tests showed that the fMRI *feelSpace* belt operates without noticeable influences on the MRI signal.

In the portable belt, the actuator core unit of the belt additionally contains an electric compass, a central control unit, power supply and management, and the identical modular piezo-driving signal generator from the MRI variant of the belt. The compass (3DM-DX-3-25, Microstrain) integrates 3-dimensional accelerometer and gyrometer inertial sensors with a magnetometer signal. It is one of the smallest orientation sensors of its kind and provides reliable and highly accurate directional information during the whole range of human movements. A custom made, Arduino-based control logic reads the compass signal and instructs the 30-channel piezo-driving board to switch on the actuator that points north. A GPS unit and data logging on a micro SD card allow quantifying the movement activity as well as the variety and regularity of the environments explored during the training. High-capacity lithium batteries provide daylong usage of the belts. A power management circuit transforms the output voltage of the batteries to the piezo driving voltage and prevents critical deep discharge of the lithium batteries. Hence, even using sophisticated piezo-ceramics as tactile actuators, the belt needs only to be charged during the night and can be used with ease during a full day.

A flexible and water-resistant fabric covers all actuators and electronic parts to provide comfortable use in both variants of the piezo-ceramic belts. Lithium batteries are extra separately encased in fireproof sacks for enhanced security of the participants.

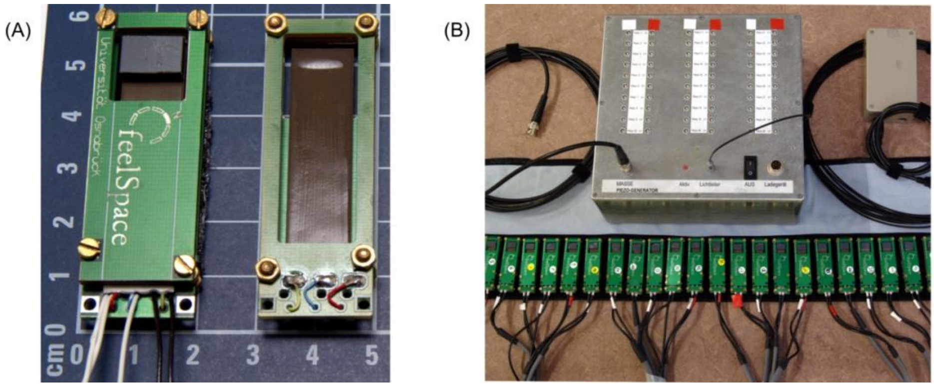

Fig 6. Details of the *feelSpace* belt. (A) Individual vibration elements feature casing, strain relief of power supply, piezo ceramic bending actuators, and a stamp. (B) The MRI compatible belt is connected by 60 coaxial cables to a filter box, which in turn is connected to the scanner room's Faraday shield. Figures taken from Keyser (Keyser, 2010) and under Creative Commons CC-BY-3 from Schumann (Schumann, 2012).

Sleep EEG Measurements

For the part of the project that involves the sleep EEG, an initial interview was conducted to exclude participants with atypical sleep patterns (shifted sleep times outside the approximate hours between 11:00 pm and 7:00 am, difficulties in falling asleep, and nocturnal awakening). One participant (BWP 8) was excluded from all sleep EEG analyses because of poor sleep quality (more than 20% of awake and 20% of stage 1 sleep in the EEG data throughout the baseline and first test night, and repeated awakening during the nights reported by the experimenter in the laboratory). Therefore, only eight participants who wore the belt (five males and three females) and five control participants were included in further analysis. All sleep measurements took place in the EEG laboratory at the Neurobiopsychology Group, University of Osnabrück. Before the start of the experiment, each participant had a 1.5h adaptation and screening nap. The nap served for participants to get familiarized with the procedure of EEG setup preparation, the sleep facility, and to reduce the "first night effect" (Agnew, Webb, & Williams, 1966). The nap was also used as a screening procedure to exclude participants from future involvement in the experiment due to problems with falling asleep in unusual or unknown environments, and any types of sleep disturbances. All participants spent four nights in the laboratory, including one baseline night. Time spent in bed was restricted to eight hours and was fixed from 11:00 pm to 7:00 am for every participant. The first night was used to collect the baseline EEG for further within subject comparison of subsequent recordings. Further nights were planned in order to obtain data over a longer period of the learning process. After this learning period, the data were used to identify effects of using the belt over time. As most noticeable effects of learning were expected in the beginning of training, recordings were scheduled tighter during the early training period. The most noticeable effect was expected to occur after the belt onset and following early training. Thus, participants spent the first and fourth nights in the sleep laboratory after the beginning of the training. The last night at the end of the training was used as the post-training measurement. Before every sleep onset in the laboratory, a sleep-wake questionnaire was used to screen participants for sleep quality and quantity, sleepiness, caffeine, nicotine, and alcohol consumption.

Sleep EEG was recorded with a Ready-to-use EEG Recording Cap for 19/21 Channels by Easy Cap™. The electrode arrangement was based on the international 10-20 system for electrode placement. Two reference electrodes were placed on the skin above the mastoid bones, ground placed at FPZ. EEG, EMG, and EOG signals were sampled at 500 Hz and acquired continuously during the night. Impedances were kept below 5 kOhm at the beginning of each recording. In addition to the EEG-recording, we used a night-vision camera in a sleeping room to control participants for body movements during the night.

Four independent judges scored sleep EEG recordings in 30 s epochs according to the standard criteria (AASM, 2007). All judges established scoring reliability among each other with above 90% agreement. EEG signals from all 10 channels were filtered between 0.5 Hz and 35 Hz, bad channels were rejected and signals were average referenced. To determine if training with the belt had an effect on sleep architecture, we compared the duration of time spent in specific stages of sleep (stage 2, SWS, and REM) from baseline to the test nights. Time spent in every sleep stage was calculated as a fraction of the whole night duration. A one-tailed paired-sample permutation test with 10^5-sample size on the sleep stages duration was applied for within- and between-group pairwise comparisons.

For further power spectral analysis, EEG recordings were visually inspected for segments containing artifacts, which were then excluded from all quantitative analyses. We performed an all-night spectral analysis on the same 30 s epochs for which sleep stages had been determined. Within each artifact-free epoch, spectral power was calculated using the routine Fast Fourier Transformation (FFT) technique for 4 electrode derivations (F3, F4, C3 and C4). Power spectra were estimated by means of the Welch method (50% overlapping with 4 s Hamming windows). We further focused our analysis on three sleep stages (SWS, REM, and stage 2 sleep) and computed average spectral density for three frequency ranges being representative for each of these sleep stages (delta: 0.5 – 4 Hz, theta: 4-8 Hz and sigma: 12-16 Hz respectively). Mean values of log transformed absolute power values for each of these frequency bands were analyzed separately with a mixed-measures ANOVA with experimental nights and electrodes derivations as within subject factors and group (belt wearing participants vs. control participants) as a between subject factor. Each significant finding was followed up with a paired t-test.

FMRI Measurements:

During fMRI measurements participants viewed a minimalistic virtual environment from a first-person perspective on a computer screen while the belt provided related tactile signals. The experiments involved *experimental participants* and *controls* performing a *homing* and a *control task* with belt *on* and *off*, *before* and *after* training. This resulted in a complete 2 x 2 x 2 x 2 design.

We used the paradigm of Wolbers et al. (T. Wolbers et al., 2007) to assess modulation of activity of brain areas involved in path integration. Participants passively traveled along two legs of a triangle and finally pointed towards the starting location with an MRI-compatible joystick (Fig 7). Instead of remembering the starting location, during control trials participants were asked to memorize the ego-centric direction of an arrow presented before the onset of the trial, and to point towards the direction of this arrow again in ego-centric coordinates after traveling along the second leg. That is, in the control condition participants experienced identical visual and belt stimulation and also performed an identical motor task, but were not asked to take into account the changes in the heading direction that are necessary in the homing condition.

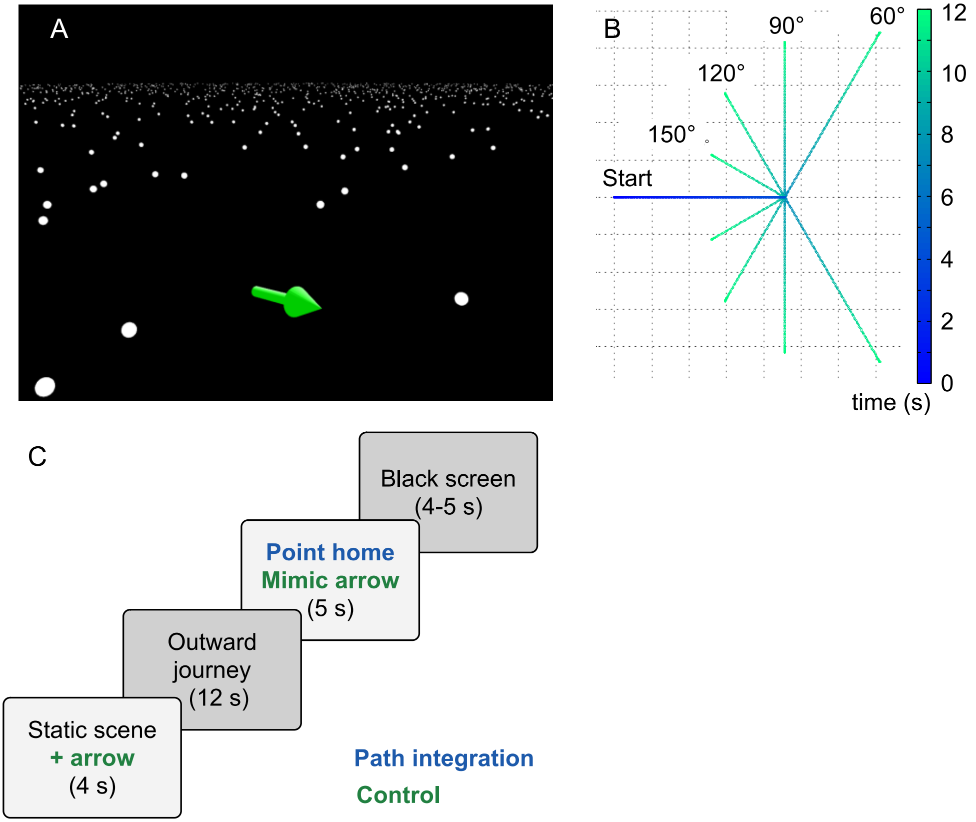

Fig 7. Schematics of the fMRI path integration task. (A) Screenshot of the virtual environment and the response arrow. A surface texture of minimal-lifetime dots provides optic flow during outward journeys. (B) Triangles used in the outward journey traveld by subjects. The first segment of each triangle had constant velocity and a duration of 4s. The length of the second segment was adjusted according to the prior turning angle to ensure a total travel duration of 12s in all trials. (C) Flow of the conditions. During path integration, subjects should point the response arrow back to the starting location. During control, subjects should replicated the angle of an arrow additionally presented at the first static scene of control trials. Figures taken from Keyser (Keyser, 2010) and under Creative Commons CC-BY-3 from Schumann (Schumann, 2012).

Participants saw a minimal visual environment from a first person perspective that provided only optic flow by a star field composed of limited-lifetime dots (Fig 7A). Virtual motion was passive to avoid confounding motor activations and to ensure identical travel durations in each trial and participant. We used eight outbound paths across all conditions. Paths were comprised of one intermediate rotation and two translations. To allow for identical onsets of the rotation period, the length of the first translation was kept constant (at 8.5 m). Intermediate rotations differed in turning direction (left, right) and turning angle (60°, 90°, 120°, 150°). Since path integration in virtual environments is most accurate when displacement velocities resemble those of natural locomotion (Ellmore & McNaughton, 2004), we used a speed of moderate walking for the translation (maximum speed 2 m/s) and the rotation (maximum speed 40°/s). Sequences of translation and rotation followed the same trapezoid velocity profile with linear increases and decreases of velocity. The plateau of the trapezoid velocity profile changed according to the length of the translation or rotation angle. To also keep total travel times constant over all trials, the lengths of the second translation were adjusted depending on the angle of the intermediate rotation, i.e., the second leg was shorter for trials with longer rotations, leading to a constant trial duration of 12 s (Fig 7B). Hence all trials had identical rotation onset times as well as total durations.

The overall study design contained a pre scanning training session of the homing paradigm outside the scanner, and the fMRI version of the homing task for the actual measurements. This allowed us to familiarize participants with the homing paradigm prior to the fMRI measurements. To minimize learning effects during the scanning further, participants also received training in virtual triangle completion in the horizontal body position outside the scanner before the actual measurements. Training sessions used a different set of triangles with different turning angles as those of the fMRI experiment. During training, trial responses were followed by instant feedback, i.e., by providing an arrow that indicated the correct direction towards the origin. Immediately before the actual measurements, participants received one additional training session of 16 trials within the fMRI environment prior to the experimental session proper. Each path was repeated five times with and five times without the belt information in pseudo-randomized order and with control of sequential effects. This yielded a total of 160 trials (80 experimental, 80 control). In the horizontal position, virtual north was arbitrarily but consistently over all trials defined in a virtual “magnetic field” displayed as if subjects had a vertical position. During travels on outbound paths, the belt signal was continually updated with respect to the direction of virtual north from the current position in the virtual space. To prepare subjects, each trial started with a static presentation of the virtual environment for 4 s that indicated the condition, followed by the outward journey that always lasted 12 s. At the endpoint of the second translation, subjects used an MR-compatible joystick to point toward the origin of the travel within a 5 s interval (Fig 7C). Pointing responses were recorded when joystick deflection exceeded 80% of maximal deflection. During inter-trial intervals, a black screen was presented randomly for 4 or 5 s. This yielded a net scanning time of 40 minutes for the experimental and the control conditions, respectively.

Visual path integration involves both the processing of self-motion cues, as well as a working memory component for changes in distance and direction from the starting point. To isolate processes of path integration, a control task was necessary that provided identical visual stimulation and motor responses, a working memory component unrelated to the path, as well as identical belt stimulation. In the final control session, subjects traveled along the same 80 paths as in the experiments. However, during the initial 4 s starting period, an arrow was presented in parallel to the ground plane and subjects were asked to remember its direction. At the endpoint of the translation, subjects had to point into the direction of the arrow shown in the beginning of the trial (Fig 7C). With the belt, path integration additionally requires somatosensory processing of the belt stimulus. Therefore, subjects also performed the control condition with and without the belt. In this control condition the global orientation aspect of the belt signal is irrelevant for the task while the tactile aspect of the belt signal is preserved. Control tasks were recorded in separate sessions to minimize the possibility that subjects engage in path integration during the control task. In summary, control trials provided identical visual and somatosensory stimulation, an identical motor response, as well as a working memory component that is unrelated to the travel path but did not require subjects to integrate the path.

For pre-processing of each MRI-run, we discarded the first five scans from further processing in order to reject remaining tissue saturation effects. The remaining scans were slice-time corrected, spatially realigned to the first volume, and normalized into MNI space using the segmented and structural image. Finally, they were spatially smoothed with an isotropic Gaussian kernel of 8mm FWHM.

In the first level design, in accordance with Wolbers et al. (T. Wolbers et al., 2007), we separately modeled the trials' 12s outbound path and 5s response periods as boxcar functions, which were convolved by SPM's canonical hemodynamic response function. A high pass filter was applied to remove baseline drifts. Each participant's data from the two measurement dates (*pre*, *post*) were modeled separately. Per date and participant, two MRI runs were recorded, interrupted by short breaks after 25min. Both runs were modeled within a single GLM, as two distinct sessions with individual intercept regressors. The regressors for outbound paths and response periods were separately defined for each level of the factors of within-subject factors *date*, *belt*, and *task.* Outbound paths with the same absolute turn values of 60°, 90°, 120° and150° were collapsed into the same regressors. Trials in which participants failed to respond within the response interval of 5s were defined as a separate regressor and excluded from analysis. Only the outbound path regressors were used for 2nd level analyses by application of the appropriate contrasts. In order to account for all our independent factors of interest (*group, date, belt, task*) in a statistically sound way, contrasts were derived from the first-level designs. Dependent on the nature of first-level statistic, these contrast images were then subjected to an appropriate second-level design using the GLMFlex extension. Specific effects were tested with the appropriate linear contrasts of the 1st level parameter estimates, and the resulting images were subsequently entered into a random effects analysis. We tested for main effects of the belt signal (*belt*), of homing (*task*), of control and belt wearing participants (*group*), as well as before and after training (*date*). The goal of this analysis was to assess the effects of all four independent factors of interest (*group, date, belt, task)* using a mixed-effects design. Input to the second level consisted of four contrast images from each participant's *pre training* and *post training* first-level GLMs: Within each first-level model and each level of *belt,* we subtracted *control task* from *path integration.*

Homing Task Measurement:

We designed an innovative homing paradigm as an alternative to the conventional triangle completion task, consisting of eight carefully crafted, complex, curvy paths. Unlike most animals, humans have a tendency to solve a homing task on simple figures via survey reconstruction. Survey reconstruction is based on a segmentation of the path into edges and angels rather than by updating of the homing vector (Fujita et al., 1993). Hence, the design of the figures was guided by the intention to trigger continuous updating in a paradigm that is less effectively resolvable by means of a configural strategy. For this purpose, complex figures without easily separable edges (= no ″landmarks″) comprising less frequent rotation angles (e.g., no 90° angles) are most suitable as these are hard to visualize mentally. While solving the homing task, participants additionally had to memorize numbers as a cognitive load.

The paths are based on non-orthogonal polygons: two rectangles, two pentagons, two hexagons, and two heptagons. None of the polygons included crossing-overs. Half of the figures were traversed clockwise, the other half counter-clockwise, with varying homing angles for each shape. The overall paths were between 15 and 18 m, not including the homing distance. As we have already a complex study design (*date*, *belt,* and *group*) on unusually difficult polygons we kept the homing segment constant in length over all figures (= 4 meters) even though in classical navigation studies, both the homing angle *and* the length of the homing segment are varied (for conventional practice, see for example (Loomis et al., 1993)). Additionally, pretests showed that participants did not realize that the length was actually always the same. Wiener and Mallot (Wiener & Mallot, 2006) demonstrated that, contrary to the predictions of most common path integration models (Fujita et al., 1993), increasing path complexity did not negatively influence path integration abilities in a speeded point-to-origin task.

Participants performed the homing task before the start of training (with or without the belt respectively) and again in the last week of training. All sessions were performed indoors, in the wind and sun shielded environment of a large hall. They consisted of two exercising runs and the subsequent actual measurements. During the whole session, participants were blindfolded and wore earplugs to eliminate both visual and auditory cues. Before conducting the actual homing measurements, participants underwent two trainings to minimize learning and habituation effects. This was achieved by familiarizing the participant with his or her environment, setting (e.g., moving freely while being blindfolded), and task. In total we collected 32 homing vectors per participant, i.e., one for each condition (*pre* vs. *post*; *belt on* vs. *belt off*) for each figure.

The general process of the homing task was similar to procedures described in classical homing studies: the experimenter guided the blindfolded participant from the origin along a path by means of the wooden handle bar, released him at the homing point, where the participant hereupon turned into the direction of origin and walked back using the shortest way. Meanwhile, the time participants needed to decide in which direction to go was recorded, until they left an area with a radius of about 40 cm around the homing point.

Additionally our participants had to solve a cognitive load task while performing the homing task. Standing at the starting point, the investigator read out a list of four numbers the participant was supposed to keep in mind during the homing task. The numbers were in a range between 1 and 40, resulting in sequences comprising two single-digit and two multi-digit numbers. When participants reached the assumed starting position, they recited the sequence of numbers.

Subjective evaluations:

To evaluate subjective experiences, we designed daily and weekly questionnaires (see also (Kärcher et al., 2012; Kaspar et al., 2014)). To assess qualitative experiences and quantitative estimations of changes we used a mixed method approach (e.g. (Tashakkori & Teddlie, 2010)). Therefore, both questionnaires contained qualitative, open-ended questions and quantitative 5-point Likert items. The daily questionnaire includes items measuring the kind and duration of activities participants performed during their daily training with and without the belt. Additionally, in the daily questionnaire sleep quality of the last night and participants' state of health, their happiness, alertness, calmness, and listlessness were assessed. Furthermore, participants were asked to write down all experiences they had during the last day. For the belt wearing questionnaire items relating to the belt were included. These items asked for how long participants wore the belt and whether technical problems occurred and if so of what kind the technical problems were. Participants were asked to report problems with the belt directly, so that a longer training outage could be avoided. The weekly questionnaire was designed to get insights into possible changes for the aspects of space perception and belt perception, and about influences of training with and without the belt, respectively. Those topics were merged into quantitative items. To get an explicit statement whether a new sense of space perception developed we included a special single item that had to be answered with yes or no in both questionnaires. These items were complemented with open-ended questions concerning changes in the perception of the belt signal (only belt questionnaire), changes of the mental map and changes in space perception (belt and control questionnaire). The questionnaires for the control participants were created in close analogy to the belt wearing questionnaire with the exclusion of the special belt signal items. Instead of reporting their experiences "with the belt", control participants were asked for their experiences after "training their orientation". In the control items the phrasing of the items was the same except substituting "with the belt" with "orientation training” in the control questions. Participants filled in the daily questionnaire each day at home. These questionnaires were collected weekly at a meeting in the laboratory where participants also completed the questionnaire and a weekly supplementary interview.

We additionally evaluated before the start of the training period the German version of the NEO-FFI (Borkenau, P. & Ostendorf, 1993) and the ACS-90 (Kuhl, 1994) to asses relevant personality traits and the “Fragebogen Räumliche Strategien” (FRS) to asses navigational behavior. The FRS was again evaluated directly after the end of the training ended and two month later. For the belt wearing group we weekly measured the AttrakDiff2 (Hassenzahl et al., 2003) Questionnaire to assess the *feelSpace* belt. These results as well as the results of the daily questionnaire and all qualitative data have been published in Kaspar et al. (Kaspar et al., 2014).

5.6 Acknowledgements

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Contributions of authors: Sabine U. König managed and supervised the study including all measurements, data analysis, and interpretation of results. She performed participant recruitment, designed, performed, and analyzed subjective evaluations, contributed to data analysis of all parts, and wrote the paper. Frank Schumann acted as project leader and supervisor in the first phase of the study and contributed on an equal basis to the development of the scientific questions. He designed and built the fMRI compatible and accompanying portable piezo-ceramic feelSpace belts, designed the fMRI experiment, contributed to the design of the homing experiment and to software development, and performed pilot experiments. He wrote the respective parts of the paper and revised the complete paper.

Johannes Keyser developed software components for the project, contributed to belt design and testing, contributed to fMRI design, performed the fMRI measurements, and analyzed the fMRI data. Caspar Goeke performed participant recruitment, contributed to building the belt, performed physiological measurements, and contributed to the sleep EEG analysis. Carina Krause contributed to building the belt, designed, performed and contributed to analysis of behavioral measurements, contributed to the respective data analysis, and the respective parts of the paper. Susan Wache performed fMRI measurements, contributed to analyzing fMRI data, and to the respective parts of the article. Aleksey Lytochkin performed and analyzed the sleep EEG measurements and wrote the respective part of the paper. Manuel Ebert performed software development, contributed to behavioral measurements, designed figures in the paper, and revised the paper. Vincent Brunsch contributed to conducting the behavioral measurements and analyzed the behavioral data. Basil Wahn contributed to the analysis of subjective evaluations and advised on statistical questions and revised the paper. Kai Kaspar contributed to the design of the subjective evaluations, advised on statistical analyses, and revised the paper. Saskia K. Nagel contributed to the study design, to sleep EEG measurements and analysis and revised the paper. Tobias Meilinger and Heinrich Bülthoff advised on and supervised the behavioral measurements and revised the paper. Thomas Wolbers and Christian Büchel advised on and supervised the fMRI measurements and revised the paper. Peter König designed and managed the study, contributed to all parts of data analysis, and wrote the paper.

6. Study Five: The Platform Study

This study has been published in “Frontiers in Behavioral Neuroscience”

Bayesian Alternation during Tactile Augmentation

Goeke, C.M., Planera, S., Finger, H., & König, P. (2016).

6.1 Abstract

A large number of studies suggest that the integration of multisensory signals by humans is well described by Bayesian principles. However, there are very few reports about cue combination between a native and an augmented sense. In particular, we asked the question whether adult participants are able to integrate an augmented sensory cue with existing native sensory information. Hence for the purpose of this study we build a tactile augmentation device. Consequently, we compared different hypotheses of how untrained adult participants combine information from a native and an augmented sense. In a two-interval forced choice (2 IFC) task, while subjects were blindfolded and seated on a rotating platform, our sensory augmentation device translated information on whole body yaw rotation to tactile stimulation. Three conditions were realized: tactile stimulation only (augmented condition), rotation only (native condition), and both augmented and native information (bimodal condition). Participants had to choose one out of two consecutive rotations with higher angular rotation. For the analysis, we fitted the participants' responses with a probit model and calculated the just notable difference (JND). Then we compared several models for predicting bimodal from unimodal responses. An objective Bayesian alternation model yielded a better prediction ($\chi_{red}^2 = 1.67$) than the Bayesian integration model ($\chi_{red}^2 = 4.34$). Slightly higher accuracy showed a non-Bayesian winner takes all model ($\chi_{red}^2 = 1.64$), which either used only native or only augmented values per subject for prediction. However the performance of the Bayesian alternation model could be substantially improved ($\chi_{red}^2 = 1.09$) utilizing subjective weights obtained by a questionnaire. As a result, the subjective Bayesian alternation model predicted bimodal performance most accurately among all tested models. These results suggest that information from augmented and existing sensory modalities in untrained humans is combined via a subjective Bayesian alternation process. Therefore we conclude that behavior in our bimodal condition is explained better by top down-subjective weighting than by bottom-up weighting based upon objective cue reliability.

6.2 Introduction

Humans sample information from their environment by many senses. In most circumstances (i.e., outside of the lab), behavior is not guided by a single modality but by a combination of several modalities. In the last decade many studies have shown that this process follows optimal Bayesian principles (Ernst & Bülthoff, 2004; Körding & Wolpert, 2004, 2006). A core concept of Bayesian integration is that perceptional noise (variance) is reduced in multimodal conditions, improving the precision of later decision processes. Many studies concentrated on the combination of visual and haptic cues. Ernst and Banks (Ernst & Banks, 2002)showed that visual and haptic information about object sizes are statistically optimally integrated. Extending this idea, Helbig and Ernst demonstrated optimal integration between vision and touch also for the shape of objects (Helbig & Ernst, 2007). Similarly, Reuschel and colleagues showed that visual and proprioceptive information are integrated in a statistically optimal manner for the perception of geometric trajectory (Reuschel et al., 2010). Moreover, several other combinations of senses have been investigated. Battaglia and colleagues found that visual and auditory information are optimally integrated in a spatial localization task (Battaglia et al., 2003). Frissen and colleagues reported optimal integration between proprioceptive and vestibular information for spatial updating (Frissen et al., 2011). Accordingly, Butler and colleagues argued that visual and vestibular signals are integrated in a Bayesian way for heading estimation (Butler et al., 2010). All in all, there is rich evidence that sensory information from different modalities is integrated following optimal Bayesian statistical principles.

While the concept of Bayesian optimal integration has been confirmed throughout several experimental paradigms, recent studies showing that integration happens only for redundant sensory information, i.e. both signals have to “describe” the same physical property. In this respect, Körding and colleagues demonstrated that the perceived causal relationship of two sensory signals is a prerequisite for sensory integration (Körding et al., 2007). Wozny and colleagues (2010) provided further evidence, sowing that the majority of their subjects used a probability matching strategy in a perceptual decision task. Furthermore, the integration of two sensory modalities requires a mapping between the two kinds of information. Mapping in this context refers to the cross-modal associations or correspondences of the sensory cues. For instance, there is a certain mapping of how it feels to hold an object in your hand and how it looks like. This association changes with the softness or weight of the object. Importantly, people can learn such a mapping, even if no prior coupling existed before. In particular, Ernst (2007) showed that subjects were able to optimally integrate visual cues (brightness) and haptic cues (stiffness). Similarly, Kaliuzhna and colleagues demonstrated that subjects integrated arbitrary co-occurring self-motion (vestibular) and visual cues (Kaliuzhna, Prsa, Gale, Lee, & Blanke, 2015). Furthermore, Kuang and Zhang introduced a new visual-olfactory mapping. In their study the researchers linked two different smells to opposite movement directions in a dot movement discrimination task. After establishing such a pairing the presentation of the olfactory cues biased the perception of visual motion direction (Kuang & Zhang, 2014). For a detailed review regarding cross-model mappings also see Ernst (2006).

If new sensory-mappings are optimally integrated without or after very short training sessions one could ask the question, do humans innately integrate two co-occurring signals? If not, what would be possible alternatives? In 2008, Nardini and colleagues tested the concept of Bayesian optimal integration in a navigation task with three different age groups: children of four to five years of age, children of seven to eight years of age, and adults. Interestingly, they found that both groups of children did not integrate optimally between visual and proprioceptive cues but rather alternated between them. In contrast, adults performed the same task in a "*Bayesian optimal*" manner (Nardini et al., 2008). Similarly, Gori and colleagues reported that integration of vision and touch before eight years of age is far from optimal (Gori et al., 2008). According to the authors, this was the case even when the dominating sense was made far less precise than the neglected sense. These results provide evidence that the capability of integrating information in a Bayesian optimal way requires several years of experience and is not an inherent property of our brain. More recently Chen & McNamara tested how people integrate visual and self-motion cues during spatial navigation and found evidence for Bayesian Alternation even for some adult subjects (Chen & Mcnamara, 2014). Besides Bayesian Alternation, there is of course the possibility that people only use one cue and completely neglect the other. However, in such a case there is no cue combination, or multisensory processing at all. In fact also other recent studies provide evidence for cue alternation behavior (Adams, 2016; De Winkel et al., 2013, 2015). The general idea behind Bayesian cue alternation is that both cues are used for the task; however, they are never used at the same time. Instead, the subject switches between one and the other cue based on a Bayesian probability selection mechanism. Hence for each trial one or the other cue is selected while the probability for selecting one cue over the other is given by the respective relative weight for each cue. In summary, several studies in the last decade found evidence for cue alternation behavior. To our understanding this deviates from the majority of findings regarding Bayesian optimal integration and needs to be investigated in more detail.

The mechanisms that underlie the transition from cue alternation to cue integration are usually observable only in children or when sensory signals are explicitly manipulated (i.e. adding sensory noise). However, it is unclear what happens when adult subjects are equipped with a new sense (or an augmented sensory-like cue). Are we able to integrate such new information with the cues we receive from our native modalities or do we have to choose and rather alternate between the two (similar as children do)? In other words, it is most interesting to examine adults' performance when they are provided with a new, augmented sense which they have to combine with information from their existing (native) senses. We specifically ask the question: Is such a process similar or different to the ones observed in children? Throughout this paper we use the term "native modality" to refer to the information mediated by angular rotation through native sensors like the vestibular system, and augmented modality to information mediated by a sensory augmentation device, even as the subjects did not receive a formal training. Angular rotation in our setup was implemented by a rotating platform on which the subjects were seated, while the augmented information was mediated via tactile stimulations (for details see the method section 6.3). Although different combinations of sensory modalities are imaginable for sensory augmentation, tactile augmentation devices have preferentially been used in many research setups (Bach-y-Rita, Collins, Saunders, White, & Scadden, 1969; Erp & Veen, 2003; Lindeman, Sibert, Mendez-Mendez, Patil, & Phifer, 2005; Nagel, Carl, Kringe, Märtin, & König, 2005; Tsukada & Yasumura, 2004). Besides academic research, the field of sensory augmentation recently also gained a lot of interest from industry. Many big companies lately introduced devices for augmented reality (e.g., Google Glasses, Microsoft Hololens, BMW Augmented Vision). However, while more products hit the market, there is a poor understanding of the underlying behavioral and neuronal mechanisms that reflect the process of combining the augmented and native senses.

Recently, Kaspar and colleagues (Kaspar et al., 2014) performed a longitudinal study with a tactile augmentation device (the feelSpace belt) and reported that subjects developed an altered perception of space after a few weeks of training. Furthermore, it has been shown that tactile augmentation is particularly useful both in a visual search task (Wahn et al., 2015) as well as when participants are deprived of visual information (Faugloire & Lejeune, 2014). Hence, for the purpose of the current study, we built a rotating platform that was linked to a tactile augmentation device. In particular, we aimed to investigate whether people instantly combine an augmented tactile sense with vestibular information on whole body yaw rotation. Also none of the participants received any training with the augmentation device, as we intended to investigate the ability to instantaneously integrate augmented and native sensory information, rather than long-term training effects. As the main goal, we then compared prediction performance for the bimodal condition between a “winner takes all” (WTA) model and three more complex models: The Bayesian optimal integration model, and two types of Bayesian alternation models, one using objective measured weights and the other using subjective weights obtained via a questionnaire.

6.3 Methods

Tactile Augmentation Device and Rotating Platform

Altogether we tested our participants in three conditions: rotating on the platform (native condition), receiving tactile vibrations around their waist (augmented condition), and both, rotating on the platform with simultaneous tactile vibrations (bimodal condition). Similarly to other setups in multimodal research, we employed a two-interval forced choice paradigm and tested participants in the two unimodal conditions (native or augmented) and the one bimodal condition (native plus augmented). Importantly, the tactile augmentation device and the rotating platform were precisely synchronized such that both signals provided redundant information. The tactile augmentation device (hereafter referred to as “tactile belt”) can, as the name suggests, be worn around the waist. An external computer controlled all 32 vibro-motors remotely via a serial port connection. The belt itself (Figure 1A) is made of a flexible fabric such that people with different abdominal sizes could wear it comfortably and the angular distance between two neighboring vibro-motors remained constant (approximately 11.25°). During the whole experiment, all participants wore the belt just above their t-shirt or undershirt so that the elicited vibrations could be felt easily. When the tactile belt was switched on, at all times exactly one vibro-motor was active. For example, a rotation of 180°

was accompanied by successive activation of half of the vibro-motors. Belt design and technology have been described in detail before (Kärcher et al., 2012; Nagel et al., 2005). To experimentally control angular rotation, we built a rotating platform with a chair fixed in the middle of it (Figure 1B). The platform could be remotely controlled, and precise parameters about angle and speed were adjusted on a trial-to-trial basis. Importantly, in the bimodal condition the vibration direction of the tactile belt was opposite to the rotation direction of the platform. In our setup, participants sat on the chair, were blindfolded, and wore headphones through which we played pink noise. Additionally, all participants held a response box with both hands, which was used for giving the required responses. They either pressed the left or the right button (indicating selection of the first or second rotation respectively). A consecutive press on a button in the middle started the next trial.

Experimental Paradigm

Overall, the trial design was similar for all three experimental conditions. Importantly, the task and the information provided was identical, however what varied between conditions was the type of sensory modality by which the information was provided. In the augmented (tactile-only) condition, only the belt vibration was activated. Here, participants had to judge angular differences purely based upon the successive tactile vibrations. In the native condition, only the platform rotated, so that the subjects had to rely only on rotational information. In the bimodal condition both the tactile belt and the platform were switched on synchronously and, therefore, subjects could use both sources of information. In all conditions, a trial consisted of two consecutive rotations (in the augmented condition only successive vibrations) with different angular sizes, with a one-second inter stimulus interval in between. The participants' task was to choose either the first or the second rotation (2 IFC task) depending on which of the two rotation angles was bigger. The participants had to press the left button to indicate that the first rotation was larger or the right button to indicate that the second rotation was larger. In fact, in half of the trials the first rotation was larger, and in the other half the second one was larger. After making their choice, the participants confirmed it by pressing the center button, whereupon which the next trial started immediately. Each trial consisted of a reference and a comparison stimulus. The reference stimulus was fixed at 146.25° (equivalent to a distance of 13 intervals between the vibro-motors) and kept constant throughout the whole experiment. The comparison stimulus varied in steps of 11.25°, the distance between two adjacent vibro-motors. The order of the reference and the comparison stimulus (i.e., which of the two was the first rotation) switched randomly on a trial-to-trial basis and was balanced overall for each subject and condition. We implemented eleven different combinations of rotation angles, ranging from five steps less than to five steps greater than the reference value (90° to 202.5°), plus the condition in which both reference and comparison stimuli were identical. Each of these angle combinations was repeated ten times in a random sequence within one modality condition. For all these trials, the speed was set constant to about 42°/s and the direction of the rotation was the same within a trial, but varied (in a balanced way) across trials. Additionally, we included ten catch trials in each condition, for which we changed the speed between the two rotations (42°/s vs. 32°/s). Contrary to the “normal” trials, in the catch trials the shorter rotation (in time) was associated with a wider rotation (in rotational angle) and vice versa. This was used to evaluate how much each condition was influenced by cognitive strategies (e.g., counting time). Catch trials and normal trials were randomly intermixed. Altogether, each condition consisted of 120 trials that were recorded in a block. Participants were offered a chance to take a short break after each set of 40 trials and a larger break after each block (condition). The breaks within one block ranged from about 20 seconds to about 2 minutes depending on the subjects arousal level. The breaks between blocks ranged between 1 to 5 minutes also depending on the subject. Each session, including all three conditions, lasted for about two and a half hours. All participants came to the lab three times, and on each visit all three conditions were measured. The order of the conditions was balanced across subjects.

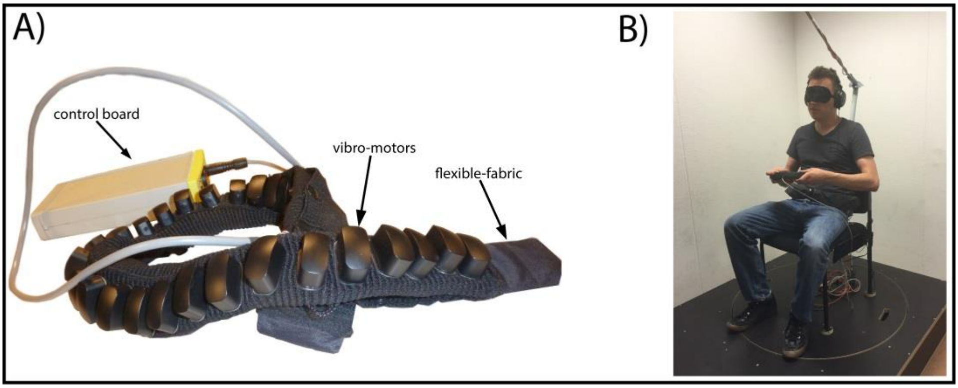

Figure 1: Sensory Augmentation Device and Rotating Platform. Panel A shows the tactile sensory augmentation device with its main components. Panel B illustrates the experimental setup. A participant is sitting on the chair fixed on the rotating platform and is wearing the tactile belt. He is additionally provided with an eye mask and headphones for noise cancellation. The participant is holding the response box in his hands.

Participants, Data Cleaning, and Questionnaire

Overall, 30 subjects were recorded within a period of about five months. However, two subjects did not complete all sessions, which left us with 28 complete data sets (16 participants were females). The age grand average of these participants was 24.03 years (SD = 3.3 years). All of the participants were students at the University of Osnabrück and each subject received either 40 euros or eight “participant hours” (which are mandatory for psychology and cognitive science students) as reimbursement for their participation. Prior to the recordings all participants were informed about the purpose of the study and signed information and consent forms. Furthermore, ethical approval was obtained by the university institutional review board. Although we tried to make the experience with the tactile belt as comparable as possible for all participants, subjective tactile sensation was arguably rather diverse. Hence, we removed the data of five participants for which the just noticeable difference (JND) could not be determined or could be determined only with very high uncertainty. These participants presumably had difficulties processing the tactile stimulus or misunderstood the task and the inclusion of their data would thereby decrease the plausibility of consecutive analysis. This procedure ensured that later analysis was based on robust measures. This left a total of 23 participants for the remaining analysis.

In addition to the two-interval forced choice task, all participants were required to fill out a questionnaire after each condition. The questionnaires were designed to find out how intuitive and difficult each condition was and how participants judged the reliability and relevance of the provided signals. Almost all questions were defined on a Likert scale (1-5) such that participants had to choose how much they agreed with a certain statement. The questionnaire was identical for the three sessions and most of the questions were also identical between conditions. For instance: “the task was difficult”, or “I was confident about my answers”. A few other Likert questions varied slightly between conditions, e.g. “The belt's signal was intuitively understandable.” vs. “The rotation signal was intuitively understandable.”, “The belt’s signal was prominent in my perception“, vs. “The rotation signal was prominent in my perception“. Besides the Likert based questions we also asked the participants to tell us which strategy they used from a fixed set of options (the complete questionnaire is provided in the appendix in section 9.2). Completing a questionnaire after each condition and session all subjects filed out 9 questionnaires in total.

Analysis

The main analysis procedure can be summarized in three main steps: First, the JND, the Point of subjective Equality (PSE), and the uncertainty of the JND for each condition and subject were estimated using a probit model. Second, based on the observed unimodal JNDs, we calculated the predicted bimodal JND (individually for each subject) for all tested models. Third, using observed and predicted bimodal JNDs, we calculated the reduced chi squared statistic (χ_{red}^2) for each model. The next two paragraphs will explain these steps in more detail. Furthermore, we describe the questionnaire analysis in section.

Curve Fitting

In order to calculate the JND, we fitted for each subject and condition a GLM with a probit link to the behavioral data. The function is formalized in Equation 1, where β_1 and β_2 are the two (optimized) parameters of the model fit and the "norminv" function computes the inverse of the normal cumulative distribution function (cdf). We needed to invert Equation 1 in order to obtain the corresponding value of angular difference (x) for a specific performance level. Then we used the asymptotic threshold of one standard deviation of a cumulative binominal distribution function (84%) as the corresponding angular difference of Equation 2 (y) and, consequently, calculated the JND. This gave us a direct measure of how precise each subject was able to distinguish the two angular stimuli from each other, separately for each condition. Next, we estimated the quality of the estimate of JNDs. Hence, we applied the error propagation method using the matrix formalism as described by Equation 3. Here U_{JND} represents the uncertainty of the JND estimation, V_β is the covariance matrix of the betas, and $J_{i,j}(\beta)$, shown in Equation 4, is the Jacobian matrix. As an example plot Figure 2 demonstrates that most of the participants showed a behavior well described by typical sigmoidal psychometric function.

(1) $$\beta_1 + x \cdot \beta_2 = \text{norminv}(y)$$

(2) $$x_{JND}(\beta_2) = \frac{\text{norminv}(y_{threshold})}{\beta_2}$$

(3) $$u_{JND} = \sqrt{\text{diag}\left(J(\vec{\beta}) \cdot V_\beta \cdot J^T(\vec{\beta})\right)}$$

$$\textbf{(4)}\quad J_{1,j}(\beta_1,\beta_2) = \frac{\partial x_{JND}}{\partial \beta_j}(\beta_1,\beta_2), j \in \{1,2\}$$

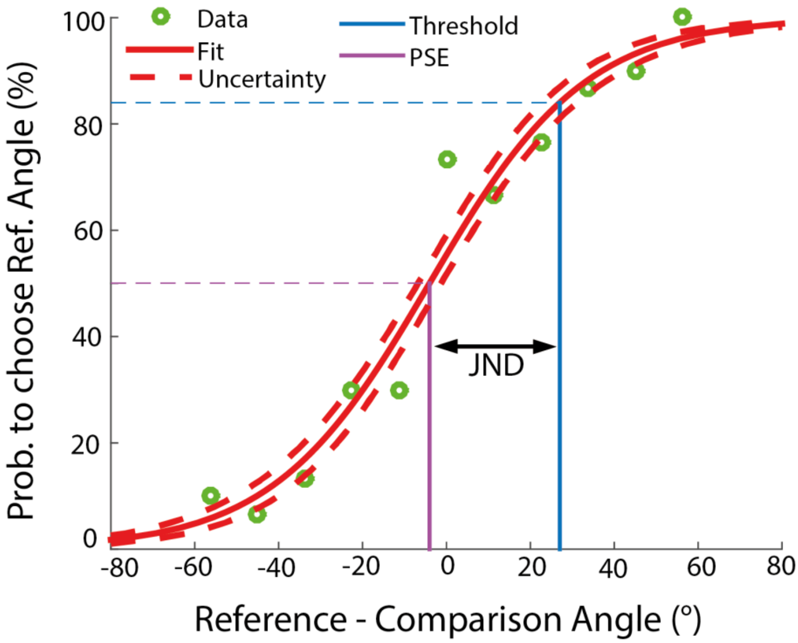

Figure 2: Example Logistic Fit (Native Condition). The figure demonstrates the performance of one participant in the native condition as an example. The abscissa illustrates the difference between the two angular rotations (reference - comparison angle) in degrees. The ordinate indicates the probability to choose the reference angle. The green circles show the recorded behavioral data, the solid red curve shows the logistic fit, and the dashed red lines indicate the uncertainty of the fit. The magenta line depicts the Point of subjective Equality, while the blue line depicts the sensory threshold, at one standard deviation (84%) of the psychometric function. The distance between the PSE and the intersection of the blue line with the abscissa represents the JND.

Model Comparison

The different models varied in their mathematical complexity for predicting bimodal performance. The simplest model was a static/intercept model which predicted always the same (mean) value for all subjects. The next one was a winner takes all (WTA) model, which took either the native or the augmented JND (depending which of them was smaller) to predict bimodal JND. The Bayesian optimal integration model and the Bayesian alternation models were more complex. The Bayesian optimal integration model can be expressed as shown in Formula 5, while the Bayesian alternation model is described in Formula 6. μ illustrates the PSE of the psychometric function while *P* stands for the probability (i.e., relative weight) of each modality. In both Formulas 5 and 6, σ represents the JND, *na* is the abbreviation for the bimodal (native plus augmented) condition, *n* equals the native-only condition, and *a* stands for the augmented-only condition.

(5) $$\sigma_{na}^2 = \frac{\sigma_n^2 \cdot \sigma_a^2}{\sigma_n^2 + \sigma_a^2}$$

(6) $$\sigma_{na}^2 = P_n(\mu_n^2 + \sigma_n^2) + P_a(\mu_a^2 + \sigma_a^2) - (P_n \cdot \mu_n + P_a \cdot \mu_a)^2$$

An interesting question regarding the Bayesian alternation model is how to determine the probabilities for the two unimodal modalities, P_n and P_a. We decided to implement two different approaches. On the one hand, we used the observed objective (although subject specific) reliabilities such that the native probability could be formulated as described in Equation 7 and, analogously, the augmented probability as in Equation 8.

(7) $$P_n = \frac{\frac{1}{\sigma_n^2}}{\frac{1}{\sigma_n^2} + \frac{1}{\sigma_a^2}}$$

(8) $$P_a = \frac{\frac{1}{\sigma_a^2}}{\frac{1}{\sigma_a^2} + \frac{1}{\sigma_n^2}}$$

On the other hand, we calculated native and augmented weights on the basis of the individual questionnaire responses. For this procedure, we selected the following eight performance relevant questions of the native and the augmented parts of the questionnaire (“I have done similar tasks before”, “The task was intuitive”, “The task was difficult,” “I think I performed well in the task”, “I was confident about my answers”, “I felt comfortable with the task”, “The belt / the rotation gave me relevant information to solve the task”, “The belt / the rotation signal was prominent in my perception”). As all these questions were answered on a Likert scale, we could directly apply mathematical operations on them. First, we averaged the responses of the three different sessions separately for each question and then subtracted answers relating to the native condition from those relating to the augmented condition. As a result, for each question we knew whether the augmented or the native task was more intuitive, difficult, and so on (positive numbers indicated higher agreement in the augmented task, negative numbers indicated higher agreement in the native task). In order to combine the responses of all questions, we applied a principal component analysis resulting in 8 different components. To further reduce dimensionality and to calculate subjective weights we then considered only the first component for further processing. Through this procedure we reduced all questionnaire responses to one scalar per subject. Finally, we normalized this number to the range of zero to one using a logistic function. These values were then used as augmented weights $P_{a.}$ The native weights P_n were then defined as the inverse 1 - $P_{a.}$ Although the complexity in terms of the mathematical expression varied between the models, we want to emphasize that we did not optimize free parameters for any model. In summary, we optimized the estimation for the observed JND, but we did not fit/improve unimodal to bimodal prediction performance by adjusting model parameters. Hence the amount of free parameters (k) was zero, and consequently the degrees of freedom (v=22=N–k-1) were constant throughout all investigated models.

Questionnaire Analysis

The main goal of the questionnaire analysis was to create a deeper understanding of the quantitative measurements. Therefore, we first looked at single questions in the unimodal parts and examined possible differences between the augmented and native ratings. Second, we analyzed the categorical responses about strategy use in all conditions in order to get a better estimate of how each participant subjectively approached the task. Here, all subjects had to choose one out of the following options: (a) tactile cue only, (b) rotation only, (c) combination of both cues, (d) counting time, (e) visualization, (f) random guessing, (g) other. We decided to focus only on these two analyses in order to keep a clear structure.

6.4 Results

Control Statistics

First of all, we aimed to investigate whether the subjects exhibited non-stationarities within and/or between sessions, for example, in the form of learning or fatigue effects. Hence, we split the data for each condition and session into the first and second “block-half” and performed three separate repeated measures analyses of variance (one for each condition) with session and block-half as independent (repeated) variables and the number of correct responses as dependent variable. Catch trials were not considered in this analysis. However, as shown in Figure 3, neither session nor block-half nor the interaction of both factors revealed a significant influence in any of the three conditions (please find the analysis of variance tables in the Appendix). This indicates that the subjects’ performances were constant within and between sessions. As the data did not reveal any indication of learning or fatigue effects, we then collapsed the data over all three sessions and calculated the amount of correct responses separately for each angle combination.

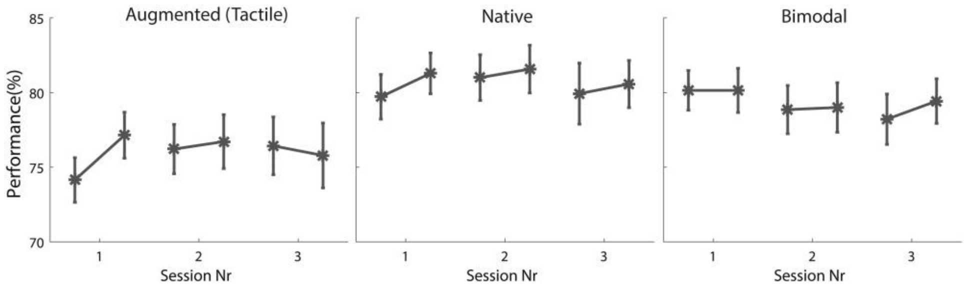

Figure 3: Investigation of Learning Effects. The abscissa divides the data of the three different sessions and the data of each session between the first half and second half of the block, separated by condition. The ordinate indicates the performance as a percentage. The error bars illustrate the average performance with the error bars representing the standard error of the mean.

Comparing Conditions

After calculating the JNDs and PSEs (see Method section 6.3), we compared both measures between experimental conditions. Figure 4A displays the results for the PSE. First we applied separate t-tests for each condition to test whether the PSE was different from zero. While for the augmented condition ($t(22) = .109$, $p = .914$) and the bimodal condition ($t(22) = -1.726$, $p = .098$) the PSE was not significantly different from zero, the native condition revealed a significant difference ($t(22)$ = -7,422, p = <.001). Furthermore, we analyzed the PSE using a repeated measures ANOVA for the factor condition, which revealed a significant effect ($F(2,44) = 7.976$, $p = .001$, partial $\eta^2 = .266$). Post hoc comparisons confirmed a significant difference between the native and the augmented PSE ($p = .001$), but no significant difference between the augmented vs. bimodal PSE ($p = .101$). The native vs.

bimodal contrast was borderline non-significant (p = .051). Importantly, as a measure of the subjects' performance we analyzed the JND; Figure 4B illustrates these results. For the statistical analysis of the JND we also applied a repeated measure ANOVA. The result revealed a main effect of condition ($F(2,44)$ = 17.869, p < .001, partial η^2 = .448). Post hoc pair-wise comparisons confirmed that the JND in the augmented condition was higher than in the native (p < .001) and the bimodal (p = .010) conditions. The JND in the bimodal condition was, in turn, higher than in the native condition (p = .003). Hence, the native condition resulted in the best performance, followed by the bimodal condition; the augmented (tactile) performance was the worst. This rather compelling result indicates that native and augmented sensory modalities were not combined in a "Bayesian optimal way", as this would require that the bimodal JND is less or equal than in either single modality. This raises the question of alternative models to be compared in the following investigation. As it is the gold standard in many studies on multisensory integration, we kept the Bayesian integration model in the model comparison procedure and compared it to several alternatives as described in the next paragraph.

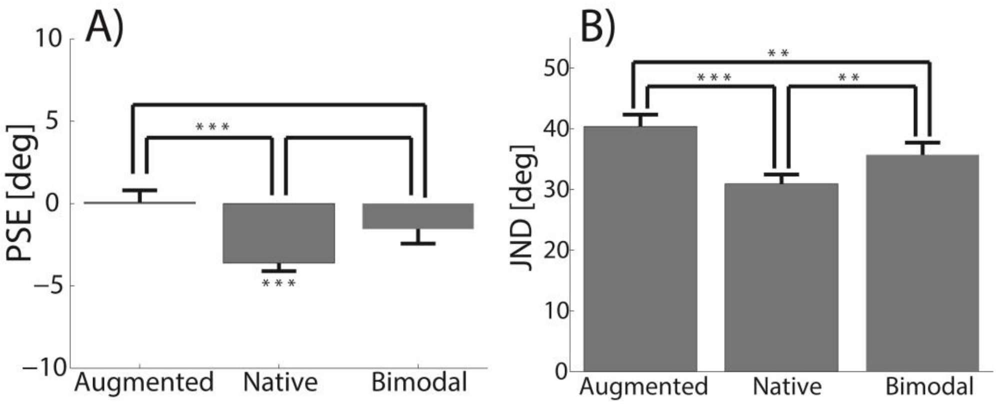

Figure 4: Comparing Conditions. Figure A shows the PSE (on the ordinate) separately for the 3 different conditions on the abscissa as a mean over subjects. The asterisks below indicate the significance level for the difference of the SPE to zero. The asterisks above show the significance level for the comparisons between conditions. Figure B shows the JND again separately for the 3 different conditions on the abscissa and as a mean over subjects. The asterisks illustrate the level of significant differences between conditions.

Model Comparison

The main goal in our study was to determine the cognitive mechanism that underlies the combination of the augmented and native sensory cues provided. To address this central question of the study, we compared the five different models in their accuracy to predict the bimodal JND given the unimodal JNDs (Intercept, Winner Take All (WTA) optimal Bayesian integration, objective Bayesian alternation, subjective Bayesian alternation). In particular, we combined the model prediction with the uncertainty measurement to calculate the reduced chi-squared value (χ_{red}^2), as shown in formula 9.

(9) $$\chi^2_{red} = \frac{1}{v}\sum_{k=1}^{n}\frac{\left(JND^2_{observed} - JND^2_{estimated}\right)^2}{\left(JND^2_{uncertainty}\right)^2}$$

This gave us a measure of how much variance each model could explain compared to the optimum ($\chi_{red}^2 = 1$), when all structure is explained and the residual variance is due to noise only. Our results show that the intercept model is a poor fit for the data ($\chi_{red}^2 = 10.95$) and leaves a lot of variance to be explained. Figure 5 summarizes the result for the other four models of interest. Although the Bayesian integration model (Figure 5A) is clearly a better model than the intercept model, it also leaves quite some variance to be explained ($\chi_{red}^2 = 4.34$). While the objective Bayesian alternation model outperformed the integration model (Figure 5C, $\chi_{red}^2 = 1.67$), the winner takes all model predicted bimodal behavior even slightly better (Figure 5B, $\chi_{red}^2 = 1.64$). However, using subjective weights for the Bayesian alternation model, prediction performance could be significantly improved such that it had the highest prediction rate and lowest residual variance among all tested models (Figure 5D, $\chi_{red}^2 = 1.09$). In fact, the χ_{red}^2 of the subjective Bayesian alternation model is very close to the optimum of $\chi_{red}^2 = 1.00$.

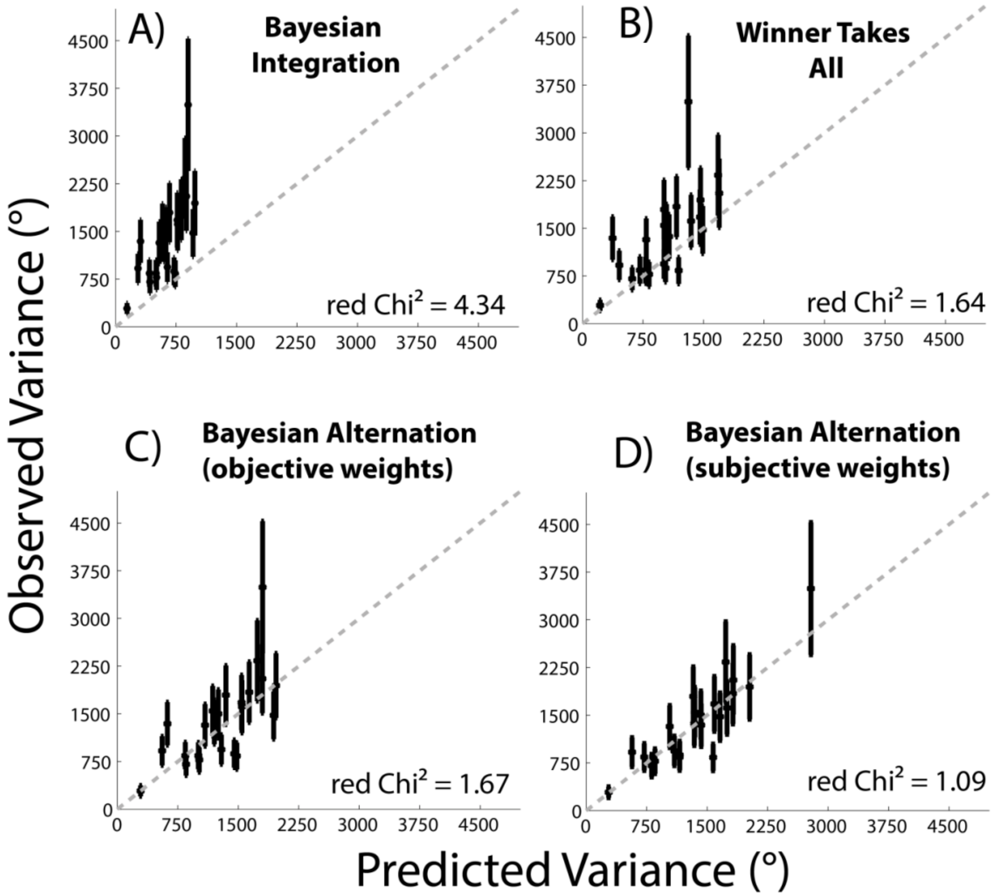

Figure 5: Model Comparison. The abscissa shows the predicted squared JND; the ordinate shows the observed squared JND in the bimodal condition. Each black dot shows the predicted versus the observed value for one subject. The error bars around the black dots illustrate the uncertainty of the observed bimodal values. The grey dashed diagonal line represents the ideal prediction. The resulting χ_{red^2} is plotted for each model.

Subjective Versus Measured Reliabilities

To better understand the differences between the two types of Bayesian alternation models, using different unimodal weights *Pn* and *Pa*, we implemented an optimization procedure to find the weights that yielded the optimal prediction accuracy for each subject (referred to as the “optimal predicted weights”). That is, we did not investigate how subjects could perform optimally, but which type of weights for native and augmented modality (per subject) would optimally explain the data as they were observed. The two weights that were used in the model comparison procedure (objective and subjective) were then analyzed against these optimal predicted weights using a linear regression. As shown in Figure 6A, the comparison of the optimal predicted weights and the objective (based on unimodal performance) weights were uncorrelated ($r(22) = .0008$, $p = .887$). In constrast, the subjective (questionnaire-based) weights showed a strong and significant correlation with the optimal predicted weights ($r(22) = .4782$, $p < .001$, Figure 6B). This result indicates that compared to the objective/measured reliabilities, the subjective evaluations (weights) better captured the intersubject variability of cue preferences.

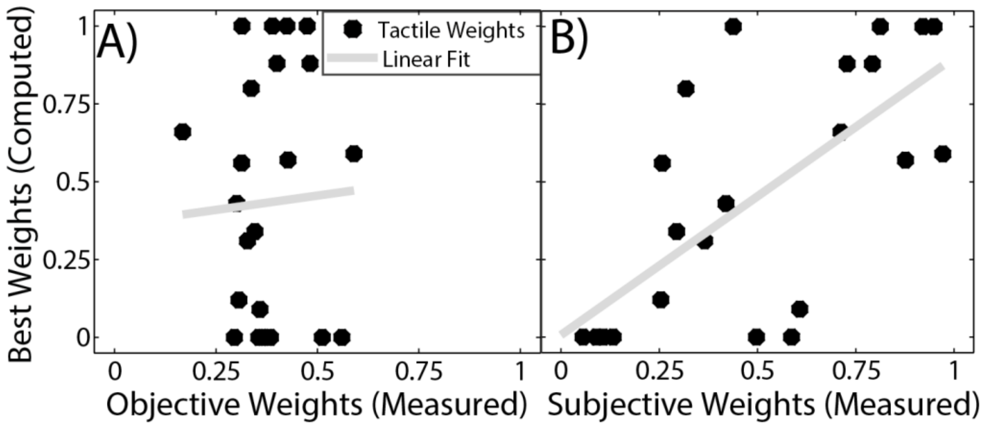

Figure 6: Correlation of Measured and Computed Weights. The ordinate shows the individual tactile weights that lead to the best possible model fit of the Bayesian alternation model. Panel A shows the correlation of the best weights and the actual measured weights based on measured reliability. Panel B shows the correlation of these estimated weights and the weights calculated from the questionnaire data. Each black dot represents one participant. The grey lines show the least square linear fit to the data.

Strategy Assessment

All participants were deprived of visual information and could not use auditory information due to the pink noise played on the earphones. As angular rotation activates the semicircular canals, which are part of the vestibular system, the main sensory input here was the vestibular modality (for that reason we use the term native modality). However, processing angular rotation without visual information might have been a rather unusual experience for many of our participants. In theory, participants could therefore have also used some more cognitive strategies like counting time or visualizing images. In order to address this question, we analyzed the catch trials and the subjective questionnaire data (directly asking for the strategy employed). For the catch trial analysis, as shown in Figure 7A, we compared the performance in three types of trials: first, the performance in the catch trials itself, which had reversed angular-time differences; second, the performance in trials with the same angular difference as in the catch trials (11.25°) but a much shorter time difference (~250 ms); and third, the performance in trials with 45° angular difference, as they were most similar in the time domain to the catch trials (~1100 ms difference), but very different in the angle domain. Figure 7B shows that in the augmented tactile task, performance in the catch trials (blue) was more similar to the trials with the same angle difference (green), compared to the trials with the same time difference (red). This supports the view that subjects used angular but not time information in this condition. However, this pattern was reversed in the native task, such that catch trial performance in the native task was more similar to same-time trials. Hence the native task was clearly influenced by time (counting) information. The bimodal task performance was again in between these two, with a trend towards the angle-based trials, supporting the idea that signal/strategy usage alternated on a trial-to-trial basis. Figure 7C illustrates the results of the subjective strategy assesment. In the respective (bimodal) question "Which strategy did you use to solve the task?" all subjects had to choose one out of following the options: belt only, rotation only, combination of belt and rotation, time counting, visual imagination, random guessing, other stategy. As the last three options (visual imagination, random guessing and other strategy) were chosen only rarely (each < 8%) we summarized them to "other strategies". Overall, the results of the questionnaire analysis are in line with the catch trial analysis. Subjects reported to have used the time information in only 8 out of 69 sessions for the augmented tactile task. In the bimodal condition, subjects reported that counting time was their preferred strategy in 12 out of 69 sessions. Again, the native task showed a reversed picture. Here participants reported that they were counting time in 38 out of 69 sessions (23 subjects * 3 sessions = 69 total sessions). Overall, both questionnaire and catch results indicate that most subjects relied on cue processing in the augmented and bimodal tasks and suggest that counting time and other cognitive strategies played a major role in the native condition.

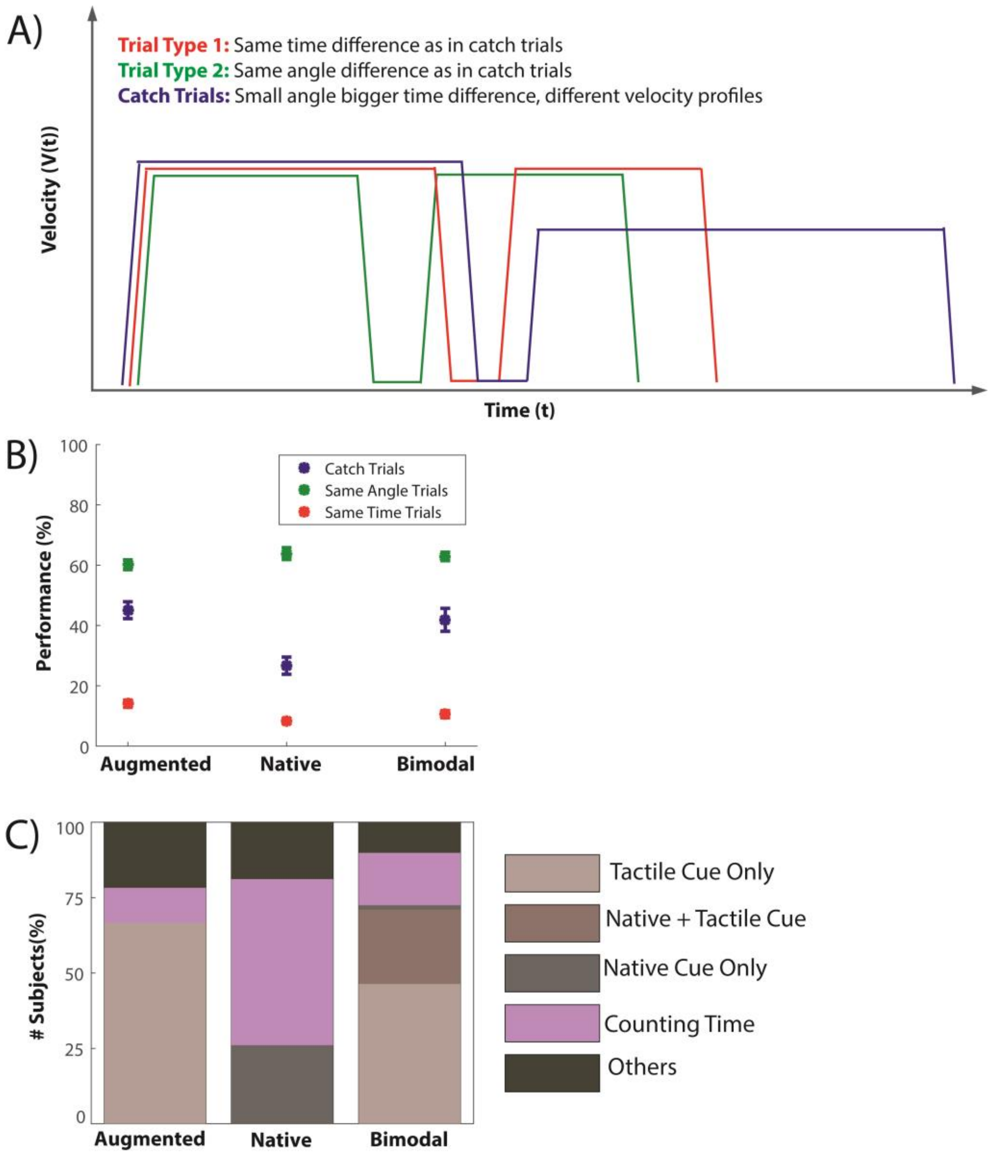

Figure 7: Strategy Assessment. Panel A displays the velocity profiles of the different trial types that were analyzed in the catch trial analysis. The green line represents a "hard trial," with small angular difference. The red line shows an easy trial with large angle (and time difference). The blue line illustrates the catch trial with inverted angle-time difference (the shorter rotation took more time). Panel B displays the result of the catch trial analysis. The abscissa separates the three experimental conditions. The ordinate illustrates average performance across

subjects. The blue error bars show the performance in the catch trials, the red error bar shows the performance for the easy trials (same time difference as catch trials), and the green error bars show the performance for the hard trials (same angular difference as the catch trials). Panel C shows the result of the questionnaire analysis regarding subjective strategy use. The abscissa again separates the three experimental conditions and the ordinate indicates the proportion of subjects using a particular self-assessed strategy. The different strategy types are color coded and labeled.

Relevance and Dominance of the Signals

As a final step, we investigated differences between augmented and tactile questionnaires for individual questions. Most questions did not reveal interesting or significant differences between the augmented condition and the native condition. Figure 8 contrasts the agreement (mean over subjects) for the following four questions between the native and the augmented condition: 1.”The belt / the rotation gave me relevant information to solve the task”, 2.”The belt / the rotation signal was prominent in my perception”, 3.”The task was intuitive”, 4.”The task was difficult”. The analysis showed that the native task was perceived as more difficult; however, the difference from the augmented task was not significant ($t(22) = -0.91$, $p = .373$). In line with this observation, subjective decision confidence was higher in the augmented condition, but again failed to reach significance ($t(22) = 1.21$, $p = .2402$). However, two other questions showed clear effects; the first was signal relevance, the other was probing signal dominance.” Participants judged the tactile belt as providing information with higher task relevance compared to the angular rotation of the platform ($t(22) = 3.34$, $p = .0030$). Similarly, the belt was rated to be perceptually more dominating ($t(22) = 4.36$, $p = .0002$) than the native information.

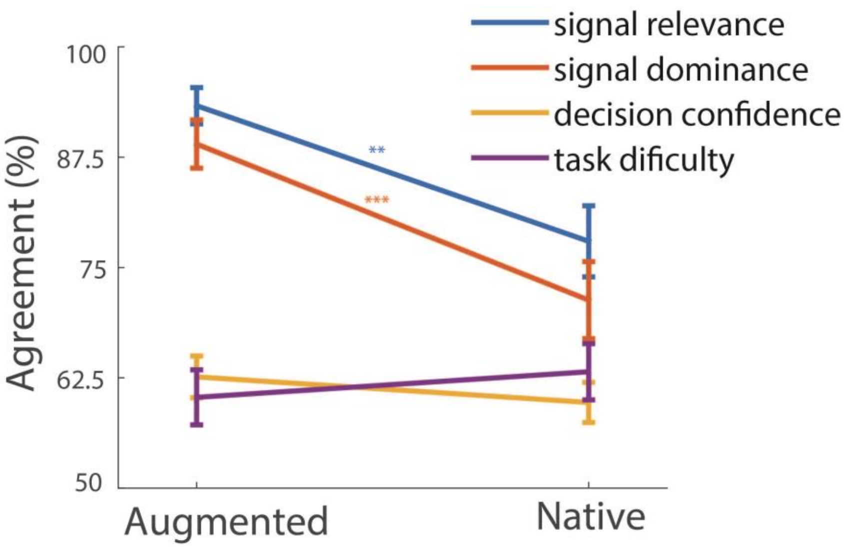

Figure 8: Signal Perception. The abscissa separates the tactile and the vestibular condition. The ordinate indicates the level of agreement for a certain question. The error bars are standard errors of the mean. The asterisks indicate the level of significant difference between the two conditions.

6.5 Discussion

Summary

We tested whether untrained adult participants are able to use augmented tactile information in a two-interval forced choice task and examined how such augmented information is combined with information from native senses. Psychometric data and consecutive statistical analysis show that all subjects were able to solve the task using only the tactile information from the augmented sense. Hence even without prior information or experience the participants were able to use the supplied augmented tactile information for the current task. The model comparison demonstrated that the subjective Bayesian alternation model had the highest prediction performance. This model reflects the idea that on each trial a subject is using one or the other sensory signal provided, caused by a (probability based) Bayesian selection mechanism. This finding is in line with earlier findings on Bayesian Alternation observed in children (Gori et al., 2008; Nardini et al., 2008). However, a more precise look at the data revealed that about half of the subjects strongly preferred one of the cues (native or augmented) while the other half used both cues more evenly. As a result, the respective weights for subjects with such strong preferences are matching a simple winner take all (WTA) strategy where these weights are set to one and zero respectively. Although such behavior could be described with a much simpler WTA model, the Bayesian alternation model yields clearly higher prediction performance on a group level. This was due to the fact that the other half of the subjects alternated between both cues more often so that this behavior was better captured with the Bayesian alternation model. Altogether one can say that the spectrum of cue preferences was rather continuous between subjects. Some subjects preferred the augmented cue, some others preferred the native cue, and again many others were in-between these extremes. To put it differently, one can consider the subjective Bayesian alternation model as an extension of a WTA strategy. In particular it is more flexible as it allows to alternate signal usage on each trial compared to each subject (but doesn't require it). Moreover, we would like to point out that this does not involve fitting free parameters, but is purely based on observed unimodal performance and questionnaire data. The difference in prediction performance between objective and subjective alternation model is of further interest. Hereby, we demonstrated that a combination of qualitative and quantitative data represents an interesting and advantageous method in the field of multimodal research.

Potential Shortcomings of the Study

One concern in the current study is related to the native modality condition. Although sensory input was provided only to the vestibular system, roughly half of the participants presumably involved a cognitive strategy such as counting time. However, the vestibular system necessarily has to integrate information over time and cannot provide an absolute reference. Hence, it would not be reasonable to assume that time information does not play any role for the vestibular system. From this perspective, we argue that the vestibular sense is to some extent a "time-angle integrator". This idea was also discussed in a study by Berthoz and colleagues (Berthoz, Israël, Georges-François, Grasso, & Tsuzuku, 1995). Furthermore, the catch trials were the hardest trials to solve with an angle-based strategy, as they not only had a very small angular difference, but also particularly long rotations (202.25° vs. 191°). Hence, subjects who aimed to use angular information in catch trials basically had to guess. As a result, some subjects might have used the counting strategy mostly in the catch trials in order to avoid guessing. Grondin and colleagues showed that humans benefit from a time counting strategy especially when judging intervals longer than 2.5 seconds (Grondin, Meilleur-Wells, & Lachance, 1999). Similarly, Clément & Droit-Volet showed that adults temporal sensitivity increases with explicit time counting, while this is not the case for children (Clément & Droit-Volet, 2006). In fact, fewer participants subjectively claimed in the questionnaire to have used a time-counting strategy as the catch trial analysis suggested. In conclusion, we argue that the native condition was influenced by both vestibular signals as well as higher cognitive strategies, in particular counting time. However, cognitive strategies did not make a major contribution in the augmented (tactile) or in the bimodal condition. Altogether, the investigation of signal/strategy use supports the idea that the majority of subjects used a subjective Bayesian alternation process to combine both sensory stimuli.

A second issue concerns the tactile belt and differences among individuals. Although we tested the augmentation device before each session, some subjects reported that they sometimes did not properly feel the vibration. Differences in waist size, position of the vibro-motors, undershirt material, and the participant's ability to differentiate tactile stimulations might have altered perception of the tactile sensation. Due to technical limitations, in some cases one or the other vibro-motor might also have vibrated less strongly than others. To counteract these issues, we removed participants for whom we could not reliably estimate the psychometric performance (JND) that was later needed in the model comparison and other analysis (as described in the method section). Our results clearly show that most subjects follow a subjective Bayesian alternation strategy for the combination of native and augmented sensory cues. However, differences among individuals were strong enough that our conclusion is reasonable for the majority of the subjects, but not for each and every individual. Weights that led to an optimal prediction showed that many participants strongly preferred the augmented cue, while other subjects had a clear bias in favor of the native signal, and still others lay in between these two extremes. Importantly, the subjective questionnaire data helped to better understand those individual differences in performance measures and time-counting strategies. All in all, subjective and objective measurements nicely match and complement each other and hereby create a more complete picture of the reported findings.

Integration vs. Alternation

Many studies suggest that human multimodal processing involves "optimal integration". Without arguing against such an overwhelming and high quality amount of empirical evidence, our findings qualify this statement to some extent. In fact, a closer look into the literature reveals that several studies reported deviations from the "standard" Bayesian integration model. One of best examples were reported by Nardini and colleagues as well as Gori and colleagues, both providing clear evidence that optimal integration is not present in children until the age of 8 years (Gori et al., 2008; Nardini et al., 2008). Most recently, Adams compared different integration models with an audio-visual temporal judgement task and similarly reported that older participants employed a partial integration strategy while younger participants (<8 years) did not integrate, but instead switched between the two sensory signals provided (Adams, 2016). Besides research with infants, there is evidence that under certain circumstances even adults do not integrate, but instead alternate between two sensory cues. In particular, DeWinkel and colleagues performed a visual-vestibular cue combination task in which adult participants were rotated around the yaw axis, given either additional visual information or not. Most interestingly, the authors reported that only about half of the participants behaved in congruence with the Bayesian integration model, while the others most likely alternated in the usage between the two cues (De Winkel et al., 2013, 2015). One of the possible explanations for both, our results as well the experiments from DeWinkel and colleagues would be that the two sensory signals were not perceived to have a common cause (Körding et al., 2007), although they were supplying redundant information. As Ernst (2007) and Kaliuzhna (2015) showed, it is possible that humans (directly) integrate two arbitrary associated sensory signals. However, combining rotational information and (augmented) tactile stimulation might require a more complex mapping than the visual-haptic associations used in these studies. An interesting idea for a follow up study of our paradigm might be to explicitly force the integration, or at least comparison of both cues. In such a scenario the information in the first interval could be provided tactilely, while for the second interval the information would be displayed via the platforms rotation (or vice versa). How well participants can solve such a task needs to be addressed in future research.

Multisensory Learning

The comparison of prediction performance between the Bayesian integration model and the Bayesian alternation model showed that participants in our study most likely alternated between using augmented and native information. Research with infants has provided evidence that optimal integration of sensory cues is not a native mechanism, but instead has to be acquired (Gori et al., 2008; Nardini et al., 2008). Moving to the other side of the age spectrum, Bates and Wolbers recently showed that the combination of visual and self-motion cues becomes less than optimal with age. The authors attribute this observation to neural degeneration in entorhinal and hippocampal regions (Bates & Wolbers, 2014). Accordingly, neural degeneration and atrophy were shown to increase with age (Dickerson et al., 2001). In general, recent studies have shown that multisensory influences arise relatively early and by a variety of mechanisms (Driver & Noesselt, 2008). In a review from 2008 Stein & Stanford argued that many multisensory neurons exist in the superior colliculus. Explicitly they showed that this region combines visual, auditory and somato-sensory input to control eye and head movements (Stein & Stanford, 2008). Burnett and colleagues tested this assumption by lesioning cats superior colliculus and conclude that damage to this area directly causes a loss of multisensory neurons which again led to a decrease of multisensory behavior (Burnett, Stein, Chaponis, & Wallace, 2004; Burnett, Stein, Perrault, & Wallace, 2007). Hence one can conclude that optimal cue integration is experience dependent and relies on intact neural structures.

While children presumably take a couple of years to successfully integrate information originating from two native modalities, it has been unclear until now how such a process is established with an augmented sense in adults. Here we provide the first evidence that the majority of adult participants combine augmented and innate sensory modalities using a subjective Bayesian alternation strategy. However, we speculate that intensive training with the sensory augmentation device could lead to a shift in the cue combination strategy. Specifically, over time Bayesian cue alternation might be replaced by optimal Bayesian cue integration, which might be associated to casual inference mechanisms described by Körding and colleagues (2007). In such a scenario the augmented tactile stimulation would improve overall performance. In line with this idea, several studies showed that training alters the individual reliabilities in a cue combination paradigm (Atkins, Jacobs, & Knill, 2001; Jacobs & Fine, 1999). Furthermore, Shams & Seitz provided striking evidence that multimodal learning is more effective than unimodal learning (Ladan Shams & Seitz, 2008). Hence, as a next step we plan to conduct a longitudinal study and investigate how training with the augmentation device will change cue combination strategies in adults.

Cue Combination and Attention

There has been a long debate whether attentional resources share a common reservoir (Jolicoeur, 1999; Arnell & Larson, 2002) or whether each modality has its own attentional resources (Martens, Kandula, & Duncan, 2010; Potter, Chun, Banks, & Muckenhoupt, 1998; Talsma, Doty, & Woldorff, 2006; Wahn & König, 2015a, 2015b,2016). In fact, attention might have played an important role also in our study. Subjects reported that the tactile stimulation dominated their perception to a significantly stronger degree than did the angular rotation. Hence the participants’ attention was driven towards the tactile stimulation. The observed Bayesian alternation process can therefore also be understood as an attentional mechanism. In this view, both cues rivaled for attentional focus such that it switched on a trial-to-trial basis, with a probability that was based on subjective reliability. In conclusion, our results support the idea of a shared reservoir of attention for native and augmented sensory cues.

A second issue is concerned with the attentional load. Several studies suggested that attentional or perceptual load modulates multisensory integration (Alsius, Navarra, Campbell, & Soto-Faraco, 2005; Mozolic, Hugenschmidt, Peiffer, & Laurienti, 2008; Klemen, Büchel, & Rose, 2009). Oppositely, Helbig and Ernst (2008) demonstrated that haptic cue weighting is independent of modality-specific attention. Similarly, Wahn and König showed the existence of optimal integration between visuotactile and audiotactile cues even under high attentional load (Wahn & König, 2015a, 2015b). In our study attentional load was not modulated; however, considering the fact that cognitive strategies such as counting time played a major role only for the native but not for the augmented condition, future investigations with varying attentional load might reveal interesting new insights.

Subjective Versus Objective Measurements of Reliability

Our results demonstrate that objective measured reliability was higher in the native condition compared to the augmented condition. Similarly, Fetsch and colleagues demonstrated that vestibular cues are overweighted in low-reliability conditions (Fetsch, Pouget, DeAngelis, & Angelaki, 2011; Fetsch, Turner, DeAngelis, &

Angelaki, 2009). However, our participants reported (subjectively) that the tactile belt provided the more relevant information for the task, and the confidence ratings were slightly higher in the tactile condition. This discrepancy between the subjective awareness of a signal's reliability and its objective reliability based on the performance measurement is surprising. A direct conclusion from such an observation is that participants in our study arguably did not represent an "objective ideal observer," which many studies have proposed as a general mechanism of sensory cue combination (Blake, Bülthoff, & Sheinberg, 1993; Ernst & Bülthoff, 2004; Landy, Banks, & Knill 2011). Opposed to that, Knill and Saunders (Knill & Saunders, 2003) introduced the concept of a "subjective ideal observer" who behaves optimally according to subjective certainty. To test such an assumption, we analyzed the subjective strategy use during the presence of both signals (bimodal condition). Interestingly, most subjects claimed to have used only the belt's signal. In that sense, subjects did not behave optimally with respect to external measurements of reliability, but indeed behaved optimally with respect to the internal subjective rating of the signal's reliability. The signal that was rated to be more relevant in the unimodal conditions was used with a higher probability in the bimodal condition.

Nevertheless, the question remains as to why subjective and objective reliability measurements differ in the first place and why the subjective reliability led to increased behavioral prediction accuracy for the bimodal task. One idea would be to look at how easily and precisely the reliabilities of the two modalities can be estimated. In particular, we assume that it is advantageous to use information which is less reliable compared to information with unknown or almost-unknown reliability (no prior), even though in the end the latter might turn out to have been more reliable. In this respect, a signal's reliability might be positively biased if it can be estimated easily and quickly. On the other hand, if a signal's reliability is difficult or time-consuming to estimate (e.g., due to the lack of feedback), it might be underestimated. We argue that the belt's reliability was relatively easy to estimate for the subjects as it provides information in an absolute coordinate system and it dominated perception according to the subjective reports (as opposed to the native condition). In contrast, the reliability of the rotation information might have been quite difficult to estimate, as the vestibular system needs to integrate information over time without an absolute reference point (Barnett-Cowan & Harris, 2009). As a result, participants might have overestimated the belt's reliability and underestimated reliability based on rotation information. If such a hypothesis holds, we believe that it can have significant consequences for research investigating cue combination mechanisms and multisensory processes.

6.6 Acknowledgements

We gratefully acknowledge support by ERC-2010-AdG #269716 - MULTISENSE and Cognition and Neuroergonomics / Collaborative Technology Alliance #W911NF-10-2-0022. Furthermore, we would like to thank the team of the Electronics Workshop of the Department of Physics of the University of Osnabrück. Together with the Fine Mechanics Workshop they built the rotating platform and the necessary electronic control elements. Here, special thanks go to Mr. Svajda and Mr. Lemme, who led the construction and the programming of the platform control, respectively. Finally, we would like to thank all members of the Neurobiopsychology Group at the University of Osnabrück, who helped in setting up the system and brining in new ideas on project report meetings.

7. Future Work & Outlook

In this last chapter I now want to provide a brief overview of what are interesting follow-up projects, which are directly linked to the outcome of the research presented in this thesis. Furthermore, I will also explain which methodological innovations I find particularly useful in that respect.

In a first follow-up project we aim to determine the neural correlates of the Bayesian cue alternation process between augmented and native sensory information described in the platform study. The technical development (synchronizing the EEG system, the rotating platform, and feelSpace belt) was quite challenging and consequently took quite some time. However, we just completed the recordings and are analyzing the data at the moment. Here, our main approach, in the EEG analysis, is to perform an independent component analysis (ICA), cluster these components, and later on compare the average activation of these clusters between the experimental conditions (i.e. bimodal vs. rotation only condition). In fact, a first look at the data looks very promising and we hope to draft a manuscript within the next 4-6 month. A second, interesting, follow-up project is the idea to test for the existence of object-to-object spatial relations (as reported in the alignment study) in a more controlled, virtual reality, setup. Thereby, the subjects will actively navigate and learn the spatial outline of a virtual city, using modern VR equipment (HTC Vive). To explicitly investigate the influence of embodied action, a second (control) group will also learn the object-to-object relations of the virtual city. However, this control group will not actively explore the environment, but learn these relations using only map-like information. We hypothesize that learning the outline of a city by active navigation (VR environment, navigation from first person perspective) yields better performance in a later retrieval task, compared to learning spatial relations based on 2D maps. Finally, we aim to extend the online-based navigation experiment, which was the basis for the first two studies presented in this dissertation. Here, two main questions are of particular importance. The first question is related to the underlying factors (origin) of the observed strategy classes. Specifically, we want to find out which socioeconomic variables can most precisely predict the strategy classes, compared the rather broad definition of “cultural background”. Hence, we will need to extend and update the questionnaire in our test. Second, we want to find out whether other well-known paradigms in spatial cognition or other scientific domains correlate with the distinction of our strategy classes. As the effect sizes for such correlations could be rather weak, online testing, with the resulting much higher samples sizes seems to be a better choice than traditional lab-based testing.

Overall, my impression is that psychology and the social sciences will benefit from two major methodological innovations within the next years. The first methodological innovation is driven by the digitalization and interconnection of scientific procedures. The internet will thereby play a major role. Our (admittedly simple) online navigation experiment demonstrated the enormous potential of online-based data acquisition. However, using the latest technology, scientists can nowadays not only share the recorded data but even work collectively on experimental designs via the internet. Furthermore, the possibility to interconnect data sets from hundreds of studies and consequently perform "big data" operations will lead to new, more valid and robust findings within the scientific community. The second major innovation is related to the increasingly better quality of virtual reality and interactive experimental setups. Until a few years ago, the overwhelming majority of laborites tested human behavior and physiology only in stationary and very artificial setups. New inventions, such as VR glasses, mobile-dry EEG systems, multi-directional treadmills, motion tracking devices, and many others, enable us to test human behavior now in a much more realistic way. As a result, I hope that we will finally create a better understanding of the embodied nature of the human mind.

8. Appendix

8.1 Acknowledgements

First of all, I would like to thank my first supervisor and longstanding mentor Prof. Dr. Peter König for his phenomenal and encouraging support. Our frequent meetings and discussions helped me a lot to develop and improve my own scientific practice. During my Ph.D., I have learned many valuable and important lessons, which will not only be important for my career, but for life in general. Especially, I am most grateful for all the granted opportunities and the freedom, which I had over the last years. Second, I also want to express my deepest thanks to my second supervisor Prof. Klaus Gramann. Although we did not work and live in the same city, I have the impression that we had a very pleasant and rewarding interaction for many years. Particularly during the process of writing the first two manuscripts, I enjoyed our frequent and lively discussions. I am sure that this will continue.

Furthermore, I want to express my thanks to all the people in the Neurobiopsychology group. Without you, my Ph.D. would have been much less exciting and much less fun than it was. I will take many enjoyable and exciting memories with me. In particular, I want to thank Jose Ossandon and Michael Ploechel who supervised my Bachelor thesis and helped me a lot during the first years in the research group. Also, I would like to thank, Holger Finger, Moritz Köster, Benedict Ehringer and Basil Wahn for their advice whenever I needed it and the great and lively scientific discussions we had over the years. Special thanks also to Marion Schmitz who was always very helpful for organizing and managing things.

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Finally, I would like to thank my family and friends for their enormous support and endless patience they brought up all these years. Without you this would not have been possible.

8.2 Disclaimer

All experiments included in this thesis confirm with the Declaration of Helsinki and have been approved by the ethics committees of the University of Osnabrück. I hereby confirm that I wrote this thesis independently and that I have not made use of resources other than those indicated. I guarantee that I significantly contributed to all materials used in this thesis. Furthermore, this thesis was neither published in Germany nor abroad, except the parts indicated above and has not been used to fulfill any other examination requirements.

8.3 Supplementary Material

Online Navigation Study

EXPERIMENTAL PROCEDURE

1. Start the video: In this experiment you will see 24 short videos of virtual passages through a star-field. After you start the experiment the first video will be loaded. When it's loaded you can start it by clicking on the arrow in the middle of the screen. The video will now start in full-screen mode. Please move your mouse cursor to the lower edge of the screen so that it disappears.

2. What you will see: All videos show passages through star- fields and each video will start with a black screen. Then a countdown will indicate the start of the passage. Every passage through a star-field starts with a straight segment and ends with a straight segment. In the middle of a passage, after the initial straight segment, there will be a turn. A turn can be to the left or to the right, or it can go up or down. Your task is to keep up orientation and to indicate, at the end of the passage, where the starting position of the passage was.

3. How you respond: At the end of a passage four arrows will appear pointing into different directions. Please select the one arrow that correctly points back to your starting position. Click on the arrow that you intuitively think is correct. When you lost your orientation during the passage please choose the arrow that you think is the most likely one. When you are done with the arrow selection, the next trial starts by loading another video.

4. Questionnaire: After the last trial there will be a short questionnaire on your experience with the experiment. Please fill out the required passages and finally press the submit button at the end of the page. Please note that during the experiment you should never use the "backward button" in your browser, since it will bring you back to the start page and all data will be lost!

FINAL QUESTIONNAIRE

Please fill out the questionnaire below. It will take you approximately 5 minutes and it's mandatory for further participation.

Age

Gender

- Male
- Female

Handedness

- Right
- Left

Occupation

Nationality

In which country did you grow up?

How much time on average do you spend on a computer per day?

- Less than 30 minutes
- less than 1 hour
- between 1 and 2 hours
- between 2 and 3 hours
- between 3 and 5 hours
- between 5 and 8 hours
- more than 8 hours

Have you ever played video games?

- Yes
- No

Do you currently play video games?

- Yes
- No

How long have you been playing video games?

- < 6 month
- 1 year
- 2–5 years

- 5–10 years
- 10 years or more

How often (approximately) do you currently play video games?

- daily
- Weekly
- once a month
- once in 6 month
- once a year
- less than once a year or never

How good do you feel you are at playing video games?

- very good
- moderately good
- not very skilled
- no skill

How confident were you about your answers?

- ➢ Very unconfident (1) - very confident (7)

Were there any problems during the experiment?

- ➢ Many problems (1) - no problems (7)

Did you like the experiment?

- ➢ No, I did not like it at all (1) - Yes, I liked it a lot (7)

How do you estimate your own spatial navigation skills?

- ➢ Very bad (1) - very good (7)

How confident are you using cardinal directions?

- Very unconfident (1) - very confident (7)

Would you like to participate in a follow up study?

- Yes
- No

Is it your first time participating in this study?

- Yes
- No

Do you have any further comments, problems or suggestions?

Platform Study

Analysis of Variance for Learning Effects

Augmented condition

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta²
Corrected Model	154,286[a]	5	30,857	,347	,883	,011
Intercept	972192,857	1	972192,857	10945,639	,000	,985
Session	19,000	2	9,500	,107	,899	,001
Half	38,095	1	38,095	,429	,513	,003
Session * Half	97,190	2	48,595	,547	,580	,007
Error	14388,857	162	88,820			
Total	986736,000	168				
Corrected Total	14543,143	167				

Native condition

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta²
Corrected Model	77,643[a]	5	15,529	,212	,957	,007
Intercept	1093517,357	1	1093517,357	14940,526	,000	,989
Session	32,714	2	16,357	,223	,800	,003
Half	36,214	1	36,214	,495	,483	,003
Session * Half	8,714	2	4,357	,060	,942	,001
Error	11857,000	162	73,191			

Total	1105452,000	168				
Corrected Total	11934,643	167				

Bimodal condition

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta²
Corrected Model	81,262[a]	5	16,252	,242	,943	,007
Intercept	1056402,881	1	1056402,881	15729,735	,000	,990
Session	60,333	2	30,167	,449	,639	,006
Half	8,595	1	8,595	,128	,721	,001
Session * Half	12,333	2	6,167	,092	,912	,001
Error	10879,857	162	67,160			
Total	1067364,000	168				
Corrected Total	10961,119	167				

Questionnaires

Augmented

Questionnaire_Tactile

I feel well.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The setup was comfortable.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The auditory noise was disturbing.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

Being blindfolded was disturbing.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was intuitive.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was difficult.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was tiring.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I felt comfortable with the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I was confident about my answers.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I think I performed well in the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

Which strategy did you use to solve the task?

○ only belt's vibration
○ counting time
○ trying to visualize the rotation
○ random guessing
○ Other:

I perceived the belt as a continuos signal.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The belt's signal was intuitively understandable.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The belt gave me relevant information about the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The belt's signal was prominent in my perception.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I used the belt's information for solving the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The belt was helpful in solving the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I felt more secure answering with the belt.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The belt's vibrations were distracting me from the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I used the following strategy for using the belt:
(please describe shortly)

Native Condition

Questionnaire_Vestibular

The auditory noise was disturbing.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

I feel well.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

Being blindfolded was disturbing.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The task was intuitive.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The task was difficult.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The task was tiring.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

I felt comfortable with the task.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

I was confident about my answers.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

I have done similar tasks before.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

Which strategy did you use to solve the task?

- only platform's rotation
- counting time
- trying to visualize the rotation
- random guessing
- Other:

I did focus on the rotation of the platform for solving the task.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The platform's rotation was disturbing.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The platform's rotation gave me relevant information for the task.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The platform's rotation made me feel dizzy.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

The platform's rotation was prominent in my perception.

Stronlgy Disagree 1 2 3 4 5 Stronlgy Agree

How many different platform's speeds did you perceive in the whole experiment?

I use the following strategy for using the platform's information: (please describe shortly)

Bimodal Condition

Questionnaire_Bimodal

I feel well.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The setup was comfortable.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The auditory noise was disturbing.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

Being blindfolded was disturbing.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was intuitive.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was difficult.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

The task was tiring.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I felt comfortable during the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I was confident about my answers.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I think I performed well in the task.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

I have done similar tasks before.

1 2 3 4 5

Stronlgy Disagree ○ ○ ○ ○ ○ Stronlgy Agree

Which strategy did you use to solve the task?

○ only belt's vibration
○ only platform's rotation
○ combination of belt and platform rotation
○ counting time
○ trying to visualize the rotation
○ random guessing
○ Other:

I perceived the belt as a continuos signal.

1 2 3 4 5

Strongly disagree ○ ○ ○ ○ ○ Strongly Agree

The belt's signal was intuitively understandable.

1 2 3 4 5

Strongly disagree ○ ○ ○ ○ ○ Strongly Agree

The belt gave me relevant information about the task.

1 2 3 4 5

Strongly disagree ○ ○ ○ ○ ○ Strongly Agree

The belt's signal was prominent in my perception.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The belt was helpful in solving the task.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

I felt more secure answering with the belt.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The belt's vibrations were distracting me from the task.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

I use the following strategy for using the belt:
(please describe shortly)

The platform's rotation was disturbing.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The platform's rotation gave me relevant information for the task.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The platform's rotation made me feel dizzy

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The platform's rotation was prominent in my perception.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

How many different platform's speeds did you perceive
in the whole experiment?

I use the following strategy for using the platform's information:
(please describe shortly)

The belt dominated my rotation's perception.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

The platform's rotation dominated my rotation's perception.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

I focused on the belt for solving the task.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

I focused on the platform's rotation for solving the task.

	1	2	3	4	5	
Strongly disagree	◯	◯	◯	◯	◯	Strongly Agree

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