# Finding Our Way Back

Pilot Experiments On the Cross-Modal Plasticity of Magnetoreception



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# Finding Our Way Back: Pilot Experiments On the Cross-Modal Plasticity of Magnetoreception

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# Abstract

This thesis investigates the potential for human magnetoreception, a sensory ability widely observed in animals for navigation using Earth's magnetic field (EMF). Although previous studies have failed to find behavioral evidence of magnetoreception in humans, recent research identified a neural response to EMF stimuli, suggesting subliminal processing of magnetic information. We hypothesize that although this sense lacks conscious perception it may still be present and trainable at an implicit level. We suggest that it may have evolved to play a role in subtle, non-navigational functions, and we explore this possibility by examining its interactions with the vestibular and visual systems. To explore the potential for training magnetoreception from implicit to explicit, we conducted pilot experiments using an aversive conditioning paradigm and introduced a sensory substitution paradigm materialized with the Magnetoreception Enhancing Sensory Substitution (MESSy) headband. This device converts magnetic stimuli into haptic feedback, aiming to train magnetoreception. In a pilot study, a 1-hour training session with the MESSy headband demonstrated crossmodal plasticity, evidenced by changes in neural sensitivity to magnetic stimuli and increased reliance on these stimuli in visual motion tasks. These preliminary findings suggest that extended training with the MESSy headband could potentially enhance magnetoreception in humans.

## Chapter 1

# Introduction

### <span id="page-6-0"></span>1.1 Background

The ability to detect magnetic fields for navigation, or magnetoreception, has been demonstrated in a wide range of animal species, including birds, fish, reptiles, mammals, amphibians, crustaceans and insects. However, humans do not possess a conscious capacity for magnetoreception. That conclusion has been established after a long period of mostly fruitless experiments on humans, and experiments that yielded inconsistent results when repeated [\(Nikita et al., 2021\)](#page-58-0). Researchers had primarily focused on testing for signs of  $ex$ plicit processing, hypothesizing that (e.g.) disturbing the Earth's Magnetic Field (EMF, or geomagnetic field) would produce observable effects on human behavior. Recent studies have identified naturally magnetic particles in the human brain, similar to those found in animals with magnetoreception [\(Kirschvink et al., 1992b\)](#page-57-0). Additionally, non-behavioral experiments have detected a strong, measurable EEG response to alterations in the Earth's magnetic field (EMF), though this response is subconscious [\(Wang et al., 2019a\)](#page-59-0). This response, known as alpha event-related desynchronization (alpha-ERD), is typically associated with the processing of external sensory or task-related information [\(Pfurtscheller and Da Silva, 1999\)](#page-58-1), and was found to be more pronounced during specific EMF rotations. While it remains unclear whether this neural response to EMF rotations is due to a sudden mismatch between vestibular and magnetic information due to their experimental setup or indicates genuine sensory processing, the evidence strongly suggests that human brains can at least implicitly process the EMF. Furthermore, neural transduction was observed only during EMF rotations with a magnetic vector corresponding to the Northern Hemisphere—where the participants resided—indicating that neural activity may be specifically tuned to process ecologically relevant EMF rotations.

### <span id="page-6-1"></span>1.1.1 Implicit vs. Explicit

The distinction between implicit and explicit processes provides a useful framework for understanding these conflicting findings. Implicit processing refers to the brain's ability to detect, analyze, and respond to stimuli without reaching conscious awareness, potentially explaining the neural responses observed in [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0). These responses suggest that the brain is processing geomagnetic information, even if this does not manifest in observable behavior or conscious perception. In contrast, explicit processing would involve the conscious perception of magnetic fields, leading to clear, measurable effects on behavior.

### <span id="page-6-2"></span>1.1.2 Human Magnetoreception as a Vestigial Sense

The interpretation of neural transduction of EMF in the absence of corresponding behavioral responses has been a subject of ongoing debate. In this thesis, we adopt the assumption that human magnetoreception may be a vestigial sense—potentially a rudimentary capability that has lost its original function through evolution. While this interpretation remains unproven, it serves as a conceptual framework for generating testable predictions. We suggest that changes in lifestyle or disruption by modern electromagnetic noise may have rendered this sense obsolete, yet the sensory apparatus may have persisted. Based on this framework, we propose that the subliminal neural detection of the EMF, as observed by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0), lacks perceptual awareness and behavioral influence because it has not been sufficiently utilized or integrated with other sensory modalities to drive its development.

It is well-established that the cortex can adapt dynamically to changes in sensory input, a consequence of neuroplasticity. For instance, [Sharma](#page-59-1) [et al.](#page-59-1) [\(2000\)](#page-59-1) redirected the visual information from a ferret's eyes to its auditory cortex, to which the ferret's brain — strikingly — rewired its auditory circuitry to interpret this information as visual. The neocortex thus seems to behave as a data-processing engine capable of rewiring itself to whatever sensory input it receives [\(Hawkins](#page-57-1) [and Blakeslee, 2004\)](#page-57-1). This strategy allows evolution to experiment with new sensory capabilities without requiring a complete redesign of neural architecture each time. It can simply repurpose what's already there. It also suggests that we don't come "pre-wired" with our senses, but these senses develop due to interaction with the environment. Studies show, for example, that color vision is not completely innate but develops over time [\(Sugita,](#page-59-2) [2004\)](#page-59-2); monkeys that were raised in monochromatic light never developed normal functioning color vision. In line with this reasoning, we hypothesize that humans inherited an ability to develop magnetoreception. However, due to factors that reduce the (need for) reliance on the EMF, it remains underdeveloped in modern humans. Factors such as electromagnetic interference from modern technology, reliance on navigation technology, or our sedentary lifestyle may inhibit its development. In essence, the principle of "use it or lose it" may have rendered this sense dormant in modern humans.

#### <span id="page-7-0"></span>1.1.3 Use It or Lose It

Consequently, in the absence of these inhibiting factors, we might be more likely to find human magnetoreception. Incidentally, linguistic studies have uncovered that a surprising number of human languages, particularly Indigenous Aboriginal languages, utilize cardinal direction systems rather than egocentric terms. For instance, native speakers of such languages might refer to their "west arm" or "north arm" rather than their "left arm." Remarkably, one culture of such individuals demonstrates an average pointing error of only 13.9°, or less than 4%, when identifying landmarks up to hundreds of kilometers away—a performance that significantly outstrips that of a Dutch control group given similar tasks [\(Levinson, 1997;](#page-57-2) [Levin](#page-58-2)[son and Levinson, 2003\)](#page-58-2). [Levinson](#page-57-2) argues that the language demands speakers to learn to encode scenes in memory with orientation and cardinal information, suggesting that such mental computations are performed subconsciously. In light of the findings by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0), we propose an alternative hypothesis: that the use of directional language (and thus also directional memory)

not only reflects magnetoreceptive abilities but also acts as a cognitive feedback mechanism, reinforcing and potentially enhancing this sensory perception through neuroplastic adaptation.

Numerous studies support the notion that language can shape perception, influencing domains such as color, smell, and sound. For instance, Russians, whose language distinguishes between lighter blues and darker blues, have been shown to distinguish these different blues faster than English speakers [\(Winawer et al., 2007\)](#page-60-1). Speakers of a tonal language, in which pitch contributes to the meaning (such as Mandarin or Thai), are better able to imitate (through singing) and perceptually discriminate musical pitch [\(Pfordresher and](#page-58-3) [Brown, 2009\)](#page-58-3). Similarly, the Jahai people of the Malay Peninsula, who have a rich vocabulary for smells, demonstrate a greater ability to identify and discriminate odors compared to English speakers [\(Majid and Burenhult, 2014\)](#page-58-4).

Historically, activities like persistence hunting may have contributed to the development of such spatial awareness and magnetoreceptive capabilities, as early humans relied on the ability to navigate vast terrains using natural cues. This evolutionary context suggests that while modern lifestyles may have diminished this sense, its potential remains embedded in the neural architecture of our recent evolutionary path. Another observation in line with this perspective is that children have difficulty using the labels "left" and "right" appropriately until around 7-11 years of age, especially when identifying the "left" and "right" of others [\(Roberts Jr and Aman, 1993\)](#page-59-3). This difficulty may indicate a natural inclination toward absolute direction over egocentric perspectives, which we lose when we learn to use egocentric terms.

### <span id="page-7-1"></span>1.1.4 Finding Our Way Back

The title 'Finding Our Way Back' reflects both the scientific and metaphorical goals of this research. Magnetoreception is a navigational tool that many animals use to find their way home, relying on geomagnetic fields for precise navigation.

Assuming that this sense may have diminished in humans due to evolutionary changes and modern lifestyles, the phrase also symbolizes our effort to explore whether this latent capacity can be reactivated and consciously developed, potentially allowing us to rediscover this ancient sensory ability.

Overall, our perspective leads to the testable prediction that magnetoreception can be trained to transition from implicit detection to explicit awareness. This thesis proposes several testable hypotheses aligned with this aim, alongside experimental results from testing them with an  $n=1$ " approach.

### <span id="page-8-0"></span>1.2 Research Questions

Our main research question is

Can human magnetoreception become a conscious sense through training?

To address this, we identified two sub-questions. Considering human magnetoreception as a vestigial sense, we may find it to have developed new minor functions, different from its original navigational function. Its neural activity might be subtly integrated with other sensory processes, potentially influencing physiology or behavior without conscious awareness. Such integration could offer pathways for transitioning from implicit to explicit magnetoreception. Therefore, the first subquestion reads

Is human magnetoreception implicitly integrated with other senses? (Chapter [3](#page-12-0))

In exploring which senses might be implicitly integrated with magnetoreception, we focused on those that are spatiotemporally linked, potentially fostering connections through Hebbian-like learning. Given that physical rotation, which activates magnetoreceptive processes, simultaneously engages vestibular and visual systems, we examined these candidate senses (Chapter [3.2](#page-13-0) and Chapter [3.3](#page-18-0), respectively).

Conversely, the second sub-question addresses the possibility of training or influencing magnetoreception to transition from implicit processing to explicit awareness, allowing for conscious perception and use of this sense

Can training affect how the human brain processes and integrates magnetoreception? (Chapter [4](#page-22-0))

As mentioned before, the main hypothesis of this thesis is that magnetoreception can be trained, potentially moving from an implicit, subconscious process to an explicit, consciously accessible sense. To investigate this claim, we have piloted two different experiments aimed at exploring its learnability.

## Chapter 2

# Preliminaries

<span id="page-10-0"></span>Here experimental details are provided that apply to all experiments in this thesis.

### <span id="page-10-1"></span>2.1 Participants

All behavioral and EEG data were collected from a single participant—the lead author—a 24-year-old male of mixed ethnicity (Danish, Indonesian, and Dutch), who is generally healthy with no known perceptual impairments.

### <span id="page-10-2"></span>2.2 Ethics

The Caltech Institutional Review Board granted permission for the lead investigators to serve as participants in the early stages of development for all the experiments in this thesis.

### <span id="page-10-3"></span>2.3 General Experimental Setup

To avoid repeating the same 'Methods' section for each experiment, we describe the general setup used in all experiments here.

### <span id="page-10-4"></span>2.3.1 Magnetic Field Manipulation Chamber

For all experiments, we used an isolated, radio frequency-shielded chamber to manipulate the electromagnetic field (EMF). Our chamber is modeled after the design described by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) (see Figure [2.1](#page-11-0) for a schematic illustration of their chamber), but with modifications to enhance portability. Specifically, our chamber is slightly smaller and modular, allowing for easy assembly and disassembly. This feature facilitates transportation and setup in various locations while preserving the magnetic shielding's effectiveness.

The chamber is equipped with three nested sets of orthogonal square coils, configured according to the four-coil design by [Merritt et al.](#page-58-5) [\(1983\)](#page-58-5). This design ensures a high degree of field uniformity in the central region of the chamber. The coils can be operated in both active and sham modes, with computer-controlled DPDT switches located in a distant control room to toggle between modes without altering the computer or amplifier settings. See Figure [2.2](#page-11-1) for details on the exact magnetic field rotations used in these experiments.

To monitor and control the magnetic field within the chamber, we employed a three-axis FVM400 handheld vector fluxgate magnetometer. This device provides precise measurements, ensuring accurate manipulation of the magnetic environment. Participants were seated in a non-magnetic wooden chair placed on an electrically isolated platform within the chamber. This setup ensured that their heads were positioned within the uniform field region, minimizing any potential electromagnetic interference. The chamber's design minimizes electromagnetic interference, providing a controlled environment for the experiments.

### <span id="page-10-5"></span>2.3.2 On Electromagnetic Interference

Electromagnetic interference (EMI) must be minimized in magnetoreception studies because radiofrequency (Rf) noise can significantly disrupt magnetoreceptive processes. Exposure to Rf noise has been shown to inhibit magnetoreception in various animals, including birds and other species, which use geomagnetic cues for navigation [\(Wiltschko](#page-60-2) [et al., 2015;](#page-60-2) Tomanová and Vácha, 2016; [Engels](#page-57-3) [et al., 2014\)](#page-57-3). Such interference can lead to negative or inconsistent results in experiments if not controlled properly. For all of our experiments, we have thus minimized electromagnetic interference, both in our experimental setup and in our participants' clothing; Participants underwent magnetic interference screening using a handheld metal detector to ensure the absence of metallic objects that could interfere with the experiment.

<span id="page-11-0"></span>

Figure 2.1: Schematic illustration of the experimental setup from [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0). Note that the experimental setup used in this thesis is a scaled-down version of the one illustrated.

<span id="page-11-1"></span>

Figure 2.2: Magnetic field rotations employed in the experiments. The duration of the rotation differed across experiments. In all experimental trials, the magnetic field intensity was maintained at a constant ambient laboratory value of approximately  $\pm 35$  µT. For all rotations, the horizontal angle varied by  $\pm 90^{\circ}$  while the inclination angle was maintained at 60° downward, consistent with conditions in the Northern Hemisphere. In some experiments, the field rotated between NE and NW (45° and -45°), and in some between SE and SW (35° to -225°).

## Chapter 3

## In Search of Sensory Cross-Talk

### <span id="page-12-0"></span>3.1 Introduction

This section addresses the research question: Is human magnetoreception implicitly integrated with other senses?, which addresses a significant gap in the literature. Previous studies primarily focused on human navigation behaviors and their disruption by electromagnetic field changes but yielded inconclusive results [\(Baker, 1981;](#page-56-1) [Baker](#page-56-2) [and Mather, 1982\)](#page-56-2). Recent work by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) has made progress by identifying an implicit neural signature associated with geomagnetic stimuli. Despite these advances, the area between low-level neural transduction and high-level navigation behaviors remain unexplored, leaving a gap in our understanding of how magnetoreception might be implicitly integrated into our sensory systems and low-level behaviors.

### <span id="page-12-1"></span>3.1.1 Neural Plasticity and Sensory Integration

Research on cross-modal plasticity, shows the brain's adaptability in reallocating neural realestate between different sensory systems in response to changes in sensory input. For instance, brief visual deprivation in sighted individuals can lead to the visual cortex processing tactile information after just a few days [\(Merabet et al., 2008\)](#page-58-6). This rapid plasticity suggests the existence of inactive neural connections between disparate sensory systems that may be activated when typical sensory pathways become unavailable [\(Clark et al.,](#page-56-3) [1988\)](#page-56-3).

Given this neural strategy to come pre-wired with a surplus of latent connections in case of sensory loss, it is plausible that human magnetoreception, even if weak, could be integrated with other sensory systems via such connections. The Bayesian brain hypothesis further supports this idea, proposing that the brain operates as a probabilistic inference machine, continuously integrating sensory inputs based on their reliability to form coherent perceptions of the world [\(Doya, 2007\)](#page-57-4). Under this framework, even subliminal geomagnetic cues could be integrated with other sensory inputs if they contribute to reducing uncertainty in sensory perception.

### <span id="page-12-2"></span>3.1.2 Proposed Hypotheses and Rationale

We hypothesize that the human brain, through a process of Bayesian inference, may implicitly incorporate geomagnetic information into other sensory modalities, particularly those that are spatially and temporally correlated with geomagnetic stimuli. Specifically, we propose that the vestibular and visual systems may be the most likely candidates for such integration. The vestibular system, which senses head motion and maintains balance, could potentially be linked to geomagnetic information as both are involved in bodily orientation. The visual system, while less directly correlated, could still benefit from geomagnetic input for tasks such as spatial orientation and motion detection.

To test these hypotheses, we have devised two experiments:

Vestibulo-Ocular Reflex (VOR) Experiment (Section [3.2\)](#page-13-0): The VOR is a critical reflex that stabilizes our vision by producing eye movements that counteract head movements. We hypothesize that the brain might recruit this geomagnetic information to enhance the VOR, especially when visual or vestibular input is compromised. We will test this by manipulating the EMF and monitoring VOR performance in a darkened controlled setting. By examining the VOR, a reflex that operates below the threshold of conscious perception, we aim to determine whether the brain integrates geomagnetic information at an implicit level.

Visual Motion Perception Experiment (Section

[3.3\)](#page-18-0): Motion perception relies on the integration of visual and vestibular information to distinguish between self-motion and the motion of external objects. We hypothesize that geomagnetic cues, processed implicitly, could be integrated into this process to enhance the accuracy of motion perception, particularly when visual information is ambiguous. This will be tested by presenting participants with random dot kinetograms (RDKs) of varying coherence levels while simultaneously manipulating the EMF and measuring their motion perception accuracy.

### <span id="page-13-0"></span>3.2 Experiment 1: Modulation of Vestibulo-Ocular Reflex by Geomagnetic Information

Abstract. Experiment 1 investigates the cross-modal integration of human magnetoreception by examining the effects of Earth's Magnetic Field (EMF) rotation on the vestibulo-ocular reflex (VOR). This study aims to understand whether changes in the EMF can elicit a measurable physiological response, assuming magnetoreception is integrated into the vestibular system. Using a controlled magnetic field manipulation chamber, the participant was exposed to both systematic EMF rotations and physical rotations while eye activity was monitored through electro-oculogram (EOG), and physical movements were tracked via a gyroscope attached to the base of the chair. The experimental design involved assessing changes in VOR both with congruently and incongruently rotating magnetic stimuli. Although results are not processed yet, a proof-of-concept experimental design has been developed.

### <span id="page-13-1"></span>3.2.1 Introduction

Vestibular information is typically thought to provide information about body position and spatial orientation in space through the vestibular system. In daily activities like walking and turning, vestibular and magnetoreceptive signals consistently overlap. We hypothesize that, since magnetoreceptive information is spatiotemporally correlated with vestibular information, it is integrated as another layer of sensory input to the vestibular system. To investigate this hypothesis, we propose a study examining a common vestibular system measure, the vestibulo-ocular reflex (VOR); this reflex stabilizes gaze during head motion. The vestibular system maintains this gaze stabilization, producing eye movement in the opposite direction of head motion [\(Gonshor, 1973;](#page-57-5) [Miles and Fuller,](#page-58-7) [1974\)](#page-58-7). The oppositely directed eye movement occurs at the same velocity as the head movement when looking at a point in space in normal conditions. In this task, we will assess the VOR during physical rotations while exposed to simulated rotations of Earth's magnetic field (in congruent and incongruent directions) to test whether the magnetic field implicitly modulates the vestibuloocular reflex, unmasking its role in our vestibular system.

### 3.2.1.1 Hypotheses

Specifically, we will assess the VOR gain measure, defined as the change in eye angle divided by the change in head angle. In normal conditions, this rotational VOR gain is 1.0, i.e. the change in eye angle is equal to the change in head angle. We postulated 2 (non-mutually-exclusive) hypotheses about how the VOR changes under the influence of magnetic field rotations.

- H1 Our first hypothesis is that the VOR gain decreases when the magnetic field rotates congruently to the subject's rotation (H1A) and increases when swept incongruently (H1B). By incongruent we mean that if the subject rotates (e.g.) clockwise, the magnetic field rotates counterclockwise. Consider the analogy that if we manipulated visual information to rotate counterclockwise to our physical clockwise rotation. In that case, we would experience an amplified rotation, rendering amplified eye movements. Thus, when rotating the geomagnetic information analogously, we have essentially amplified the subject's physical rotation, and thus expect an increased VOR gain. By the same logic, in the congruent case, we expect a decreased VOR gain.
- H2 The second hypothesis is that, due to the introduced discrepancy between vestibular and magnetoreceptive information, the corrective eye movement happens with a slight delay, as the brain needs some time to resolve this ambiguity.

In Figure [3.3](#page-15-0) we illustrated these hypotheses for clarity. Note that eye velocity will always be the opposite of the head velocity when maintaining gaze, which is why we use the inverted eye velocity to visualize their hypothesized relationship more intuitively.

### <span id="page-14-0"></span>3.2.2 Methods

### 3.2.2.1 Stimuli and Procedure

Participants were seated in the center of a radio frequency-shielded chamber, described in Section [2.3,](#page-10-3) on a specially designed rotating wooden chair. The chair was controlled manually by an experimenter using a pulley system from outside the chamber. Since the intended measure—VOR gain—is the ratio between the change in eye movement and head movement, the absolute speed of rotation was not a critical factor, justifying manual rotation despite its inconsistent speed. The rotating chair was constructed with non-magnetic materials to eliminate electromagnetic interference (see Section [2.3.2](#page-10-5) for rationale), and participants were instructed to keep their feet off the ground to avoid any tactile feedback during rotations. The environment was completely darkened to eliminate external sensory cues, ensuring the only sensory input came from the experimental setup.

During each trial, the magnetic field's declination was rotated 90° between the southeast (SE) and southwest (SW) directions (135° to - 225° in our magnetic field coordinate reference frame) while maintaining a constant downward inclination of  $+60^{\circ}$ , consistent with the Northern Hemisphere's geomagnetic orientation. The magnetic field rotation was synchronized with the participant's physical rotation, both occurring over a 3000-millisecond period, followed by a 2000 millisecond inter-trial interval. We opted for a 3000-millisecond magnetic field rotation duration instead of the 100-millisecond duration used in the original experiment by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) because manual rotation of the participant took approximately 3000 ms. Field rotation direction is randomly presented from one of three conditions, right rotation, left rotation, or fixed (no rotation).

As a workaround for tracking the participant's head position, a MPU-9250 gyroscope sensor was attached to the bottom of the rotating chair, providing data on rotational speed while minimizing electromagnetic interference. The gyroscope of the MPU-9250 has a maximum low-pass filter response at 250 Hz. Eye movement was monitored using electrooculogram (EOG) facial electrodes connected to a BioSemi Active Two Amplifier, enabling the measurement of the vestibulo-ocular reflex (VOR) without the need for traditional eye trackers.

The experiment comprised 46 trials in total, with magnetic field rotation sequences designed to be pseudo-random. The participant's task was to remain still and maintain their gaze on a fixed point directly in front of them (when facing South, i.e. 180°) while the experimenter manually rotated the chair. The start of each trial was indicated by an audio tone, signaling both the initiation of the magnetic field rotation and the physical rotation.

### 3.2.2.2 Data Collection

Continuous EEG was recorded from 4 electrodes using the BioSemi Active Two Data Acquisition and Amplifier System. Horizontal electrooculogram electrodes were placed adjacent to the outer canthi and were used to record horizontal eye movements. Two vertical electrooculogram electrodes were placed above and below the right eye to record vertical eye movements to capture the vestibulo-ocular reflex.

### 3.2.2.3 Data Analysis

Offline analysis was performed using EEGLAB [\(Delorme and Makeig, 2004\)](#page-56-4) and ERPLAB [\(Lopez-](#page-58-8)[Calderon and Luck, 2014\)](#page-58-8). Data were resampled at 250 Hz. A noncausal Butterworth bandpass filter was applied (half-amplitude cutoffs  $= 0.1$  Hz and 15Hz, slope  $= 12$  dB/octave).

### <span id="page-14-1"></span>3.2.3 Results

At the time of writing, we have not yet completed the data analysis. The methodology presented challenges, including varying sample rates across the data and the manually controlled, noisy rotation. However, we have included two preliminary sample trials for reference. In Figure [3.5,](#page-17-0) the red line represents head velocity, while the blue line indicates eye velocity. At face value, there is a visible difference between the congruent and incongruent condition.

### <span id="page-14-2"></span>3.2.4 Conclusion

The challenges in analyzing and interpreting the results suggest that a different approach is necessary for future iterations of this experiment. Implementing a controlled mechanical rotation could significantly reduce noise. Additionally, due to the subtle nature of the vestibulo-ocular reflex (VOR), a reliable measurement apparatus with a high sampling rate is essential. At this stage, we are unable

<span id="page-15-0"></span>

Figure 3.1: Hypothesis 1a - Head and inverted eye velocity in the congruent condition. The magnetic field is rotated in the same direction as the subject's rotation, rendering a decreased rotation. The eye velocity is then expected to decrease with respect to the head velocity, and VOR gain is thus <1



Figure 3.2: Hypothesis 1b - Head and inverted eye velocity in the incongruent condition. The magnetic field is rotated opposite to the subject's rotation, rendering an increased rotation. The eye velocity is then expected to increase with respect to the head velocity, and VOR gain is thus >1.



Figure 3.3: Hypothesis 2 - In both the congruent and incongruent case, we would see that the VOR reflex is initiated slightly later, due to the sensory conflict between magnetic and vestibular information.



(a) The MPU-9250 sensor soldered on a breadboard, connected to a Teensy 4.0, and powered by a LiPo battery (LiPo not included in the image)



(c) The gyroscope sensor was mounted to the bottom of the rotating chair, wrapped in copper foil to eliminate RF interference.



(b) The participant wearing the 4 electrodes recording EEG using the BioSemi Active Two Data Acquisition and Amplifier System.



(d) The pulley system as seen from the point of view of the experimenter. By alternately pulling the cords, the chair would rotate 90 degrees.

Figure 3.4: Additional images of aspects of the experimental setup.

<span id="page-17-0"></span>

(a) A sample VOR response in the congruent condition.



(b) A sample VOR response in the incongruent condition.

Figure 3.5: Example VOR trials in the congruent (a) and incongruent (b) conditions. The red line represents head velocity, while the blue line represents eye velocity.

to draw any definitive conclusions. If the experimental setup proves successful, a promising direction for future research would be to include participants with vestibular dysfunctions. Their VOR might benefit from the integration of geomagnetic information, potentially restoring the accuracy of their VOR by compensating for the inherent noise in vestibular signals.

### <span id="page-18-0"></span>3.3 Experiment 2: Modulation of Visual Motion Perception by Geomagnetic Information

Abstract. Motion perception depends on the integration of visual and vestibular information to differentiate between self-motion and the movement of external objects. We hypothesize that geomagnetic cues, even when subliminal, might be integrated into this process to improve motion perception accuracy, especially under ambiguous visual information conditions. To test this hypothesis, we presented a participant with random dot kinetograms (RDKs) at varying levels of coherence while simultaneously manipulating the Earth's magnetic field (EMF) and measuring motion perception accuracy. Although the study is preliminary  $(n=1)$ , we observed a subtle influence of geomagnetic information at 60% visual coherence. The directionally biased effect of geomagnetic cues suggests a potential integration of vision and magnetoreception in an ecologically relevant manner.

### <span id="page-18-1"></span>3.3.1 Introduction

To interpret the world effectively, the brain integrates evidence from multiple senses, enhancing perceptual judgments when sensory information agrees. Vision is typically the most reliable sense for perceiving motion; however, when visual information is unreliable (i.e. due to darkness or occlusion), other senses are recruited to aid perception. Numerous studies have shown that auditory motion can influence the perception of visual motion, especially when visual cues are ambiguous [\(Meyer](#page-58-9) [and Wuerger, 2001;](#page-58-9) [Hidaka et al., 2011;](#page-57-6) [Berger and](#page-56-5) [Ehrsson, 2016\)](#page-56-5). Even ecologically irrelevant audio like pitch can influence the perception of up/down visual motion, as can linguistic signals (i.e. hearing "left" vs "right") [\(Sadaghiani et al., 2009\)](#page-59-5).

To further investigate this idea, we examined magnetoreception's influence on visual motion perception, aligning with our goal of determining whether implicit magnetoreceptive processing can impact explicit sensory perception. Given that [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) found implicit detection of the geomagnetic field, we speculated it might influence visual motion perception, especially if visual information is ambiguous. Visual motion perception relies on the integration of visual and vestibular information to distinguish between self-motion and the motion of external objects. We hypothesize that geomagnetic cues, even when processed implicitly, might be integrated into this process to enhance the accuracy of motion perception. We employed an RDK task to test visual motion perception at two coherence levels (0% and 60%) during a magnetic field rotation. Participants report the direction of visual motion using a left-right button press.

#### 3.3.1.1 Hypothesis

We hypothesize that magnetoreceptive motion information may influence visual motion reports. Specifically, we expect the magnetic field rotation to have a greater influence on participants' reports of visual motion during the 0% coherence condition, where no coherent visual motion information is provided, compared to the 60% coherence condition. Given that the magnetic field is generally perceived as stable, we hypothesize that a perceived magnetic rotation to the left, for instance, would lead to a greater likelihood of visual motion being perceived in the opposite direction, to the right. Analogously, if the horizon were to suddenly move upwards, it would more likely be perceived as the surroundings falling downward. In other words, we hypothesize that participants will be more likely to report visual motion in the opposite direction as the magnetic field rotation (i.e. incongruent with it).

#### <span id="page-18-2"></span>3.3.2 Methods

#### 3.3.2.1 Stimuli and Procedure

Participants are seated in the center of the electrically shielded chamber (as described in Section [2.3\)](#page-10-3) on a wooden chair. A computer monitor is placed on the outside of the tent/chamber and can be viewed through a copper mesh RF-shielded "window" on one side of the chamber (the East side in our magnetic field coordinate reference frame) at a viewing distance of 100 cm (see Figure [3.7](#page-20-0) for images).

On each trial, participants are asked to fixate on a central dot and are presented with an RDK for 350 ms (see Figure [3.6](#page-19-2) for a schematic illustration of trial logic). The direction of motion is randomly sampled from sixteen possible orientations within 30 degrees of the cardinals for left and right responses. Motion coherence was either 60% or 0%. After the RDK ended participants were presented with a prompt that asked them to re-

<span id="page-19-2"></span>

Figure 3.6: Schematic illustration of the trial logic.

port whether the direction of motion was to the right or the left using a button box in the chamber. Concurrently, with the subject facing East, the magnetic field declination was rotated between NE and SE (45° and 135°) while the inclination was held downwards at  $+60^{\circ}$ . The magnetic field rotation was presented for 100 ms. Field rotation direction is randomly presented from one of three conditions, right rotation, left rotation, or fixed (no rotation). The stimuli were presented in 2 blocks of 150 trials, separated by a short break. Participants were presented with 50 right rotation, 50 left rotation, and 50 fixed trials randomly intermixed

### <span id="page-19-0"></span>3.3.3 Results

The results of the visual motion perception task under geomagnetic influence are illustrated in Fig-ure [3.8.](#page-21-1) Preliminary data  $(n=1)$  showed differences between the congruent condition (visual motion direction and magnetic field direction align) and the incongruent condition (visual motion direction and magnetic field direction are opposite). These results are consistent with our hypothesis that visual motion is more likely perceived in the opposite direction as the magnetic field rotation. This effect is more pronounced in the 60% coherence condition, where there is subtle visual information.

### <span id="page-19-1"></span>3.3.4 Discussion

While the findings of this study should be cautiously interpreted due to the limited sample size  $(n=1)$ , they offer valuable insights into how the brain integrates sensory information under varying levels of reliability and awareness. We initially hypothesized that as visual information became less reliable, the brain would increasingly depend on alternative inputs, such as geomagnetic cues. However, the observed pattern—where geomagnetic influence was stronger in the 60% coherence condition than in the 0% coherence condition—deviates from this expectation.

This deviation can perhaps be understood through the Bayesian brain framework [\(Doya,](#page-57-4) [2007\)](#page-57-4). In typical scenarios where both auditory and visual cues are consciously perceived, the brain weighs these inputs according to their reliability. As visual motion becomes less reliable, auditory cues are recruited more heavily. However, in the context of this experiment, where geomagnetic cues likely function below the threshold of conscious perception, the brain may require the visual stimuli to be closer to or exceed the perceptual threshold for effective integration with geomagnetic cues.

At 0% coherence, the visual information was too unreliable to form a clear perception of motion, and the geomagnetic cues were likely too weak to influence perception, resulting in minimal effect. In contrast, at 60% coherence, the visual motion provided a somewhat reliable signal. In this context,

<span id="page-20-0"></span>

(a) View of the computer screen from inside the magnetic field manipulation chamber. The coppershielded window introduces some visual artifacts, which, based on pilot testing, did not interfere with the experimental procedure.



(b) Outside view of the magnetic field manipulation chamber, with the computer screen placed to be seen from within the chamber.



(c) The utilized button box.

Figure 3.7: Additional images of aspects of the experimental setup for the visual motion perception task, inside (Figure [3.7a\)](#page-20-0) and outside (Figure [3.7b\)](#page-20-0) of the experimental chamber .

<span id="page-21-1"></span>

Figure 3.8: Proportions of congruent and incongruent responses to the magnetic field rotation at 0% and 60% coherence levels combined into a single bar chart.

additional geomagnetic cues could be integrated, altering the perception of the visual input. This suggests that the brain may be summing probabilities from both visual and geomagnetic cues, allowing them to collectively surpass the threshold for conscious influence on motion perception.

Incidentally, [Ramos-Estebanez et al.](#page-59-6) [\(2007\)](#page-59-6) demonstrated that when visual and somatosensory stimuli were presented in close spatial and temporal proximity, they could combine to reach perceptual awareness, even if each stimulus alone was below the perceptual threshold. Similarly, [Wuerger](#page-60-3) [et al.](#page-60-3) [\(2003\)](#page-60-3) found improved motion detection when motion signals were presented at threshold levels in both visual and auditory modalities, compared to just one. This improvement is best explained by probability summation, where the auditory and visual stimuli are processed independently in their respective pathways and then integrated at a decision-making stage.

The results showing a higher proportion of visual motions perceived in the opposite direction to the magnetic field rotation aligned with our initial hypothesis. This finding was further replicated in additional unpublished testing by [Krisst et al.](#page-57-7)  $(2024)$  with 13 subjects, even under the 0% coherence condition. Together, these outcomes suggest that the brain integrates not only vestibular but also geomagnetic information to assess bodily rotation, leading to the perception of dots drifting in the direction opposite to the manipulated geomagnetic reference frame.

#### <span id="page-21-0"></span>3.3.5 Conclusion

The study revealed that magnetoreception is indeed implicitly integrated into visual perception. An unexpected pattern was found in which geomagnetic influence was stronger at 60% visual coherence than at  $0\%$ , contrary to our initial hypothesis. This suggests that when visual information is moderately reliable, the brain may integrate subtle geomagnetic cues through a process akin to probability summation, allowing them to collectively surpass the threshold for conscious influence on motion perception. Additionally, the participant was more likely to perceive motion in the opposite direction as the magnetic cue rotated. We propose that — because geomagnetic information is perceived as a stable reference cue  $-$  a geomagnetic rotation to (e.g.) the left would lead to visual motion being more likely to be perceived in the opposite direction, to the right. The data thus suggest ecologically relevant connections between vision and magnetoreception. While these results are intriguing, they should be interpreted with caution due to the study's limited sample size. This finding was, however, further replicated in additional unpublished testing by [Krisst et al.](#page-57-7) [\(2024\)](#page-57-7) with 13 subjects. Overall, the results indicate implicit sensory integration between vision and magnetoreception.

Future research should explore multiple intermediate levels of RDK visual coherence to better understand how geomagnetic information influences visual motion perception across different levels of visual reliability. Additionally, varying the timing of RDK presentation in relation to magnetic rotation could provide further insights into the integration of magnetoreception with vision. Finally, testing participants with vestibular dysfunction could be particularly informative, as their reliance on geomagnetic cues might be heightened due to their impaired vestibular system, potentially affecting their perception of visual motion under geomagnetic manipulation.

## Chapter 4

# On Training Magnetoreception

<span id="page-22-0"></span>"Any man could, if he were so inclined, be the sculptor of his own brain."

— Santiago Ramon y Cajal

### <span id="page-22-1"></span>4.1 Introduction

In Chapter [3,](#page-12-0) we explored the question Is human magnetoreception implicitly integrated with other senses? by investigating the possibility of sensory cross-talk between magnetoreception and our known senses. With the long-term goal of enhancing human magnetoreception from implicit detection to explicit awareness, our first objective is to answer the question Can training affect how the human brain processes and integrates magnetoreception?. In other words, we seek to understand the extent of neuroplasticity in the circuits potentially involved in human magnetoreception. To address this, we piloted two approaches that leverage implicit learning to reveal the potential for human magnetoreception: conditioning (Experiment 3) and sensory substitution (Experiment 4).

#### <span id="page-22-2"></span>4.1.1 Neurally Associating

The first approach, conditioning or associative learning, is a well-established method for probing the sensory capabilities of animals. Believed to have originated in early Bilateria, conditioning is one of the most fundamental forms of learning. It involves forming associations between initially neutral stimuli and biologically significant stimuli, such as a positive or negative reward. After repeated pairings, the neutral stimulus alone becomes a predictor of the significant stimulus. This learning process is widely observed across various species, highlighting its evolutionary significance [\(Bennett, 2021\)](#page-56-6). Given the fundamental nature of conditioning, we aim to utilize this mechanism to explore the potential for conditioning human magnetoreception.

The second approach, sensory substitution (SS), leverages cross-modal plasticity to convey information typically processed by one sense through another. Traditionally, this method has been studied in the context of compensating for a lost or damaged sense, such as providing artificial hearing to the deaf [\(Perrotta et al., 2023\)](#page-58-10) or sight to the blind [\(Bach-Y-Rita et al., 1969;](#page-56-7) [Ward and Meijer,](#page-60-4) [2010\)](#page-60-4). In some cases, a sensory substitution device can even rehabilitate an impaired sense, leading to lasting changes after the device is removed. Viewing the task of learning magnetoreception as a form of rehabilitation, we propose a novel method called magnetosensory substitution (MSS). This method aims to train the remnant sense as a sense, potentially inducing enduring neuroplastic changes through extended training.

### <span id="page-22-3"></span>4.1.2 Proposed Hypotheses and Rationale

For the conditioning experiment, we hypothesize that by repeatedly pairing magnetic field changes with a biologically significant stimulus (such as a mild electric shock), the brain can be conditioned to recognize and respond to magnetic fields.

For the magnetosensory substitution experiment, we hypothesize that providing feedback corresponding to magnetic field changes through a sensory substitution device can train the brain to integrate and utilize magnetic information as a navigational cue.

### <span id="page-23-0"></span>4.2 Experiment 3: Fear Conditioning Geomagnetic Stimuli

Abstract. The potential for conditioning human magnetoreception was observed through the pairing of geomagnetic cues with auditory stimuli and a shock. A single participant underwent conditioning where ecologically relevant magnetic field rotations were paired with an auditory cue, after which the auditory cue was gradually attenuated. Electrodermal activity (EDA) was measured to assess changes in sensitivity to magnetic stimuli. The results were inconclusive, likely due to the limited number of trials and small sample size, indicating the need for alternative approaches in conditioning human magnetoreception.

### <span id="page-23-1"></span>4.2.1 Introduction

Classical conditioning occurs when a neutral stimulus (conditioned stimulus, CS) is paired with an unconditioned stimulus (US) that elicits a natural response. Over repeated pairings, the CS alone can elicit a response similar to the one originally produced by the US, i.e. a conditioned response (CR). This experiment seeks to determine whether a simulated geomagnetic field (CS) can be associated with an aversive electric shock (US) to elicit a conditioned physiological response.

Traditionally, conditioned stimuli (CS) in classical conditioning experiments are consciously perceived, which raises concerns about using the magnetic field as a CS in this study, as it is only perceived subconsciously. This lack of conscious perception could undermine the conditioning process. However, some studies have demonstrated that associative learning can occur without conscious awareness of the CS. For instance, research involving backwardly masked salient visual stimuli has shown that fear-relevant stimuli can still induce learning even when they are not consciously perceived [\(Esteves et al., 1994;](#page-57-8) [Wong et al., 1997\)](#page-60-5). Similarly, studies on patients with blindsight, a condition where individuals can respond to visual stimuli despite cortical blindness, have shown that fear conditioning to visual cues can occur without perceptual awareness [\(Hamm et al., 2003\)](#page-57-9). However, while these findings support the possibility of conditioning with subconscious stimuli, they primarily involve fear-relevant stimuli (vision) and may not be fully generalizable to other sensory modalities, such as magnetoreception.

Through personal communication with Kirschvink, we learned of his unpublished experiment involving a variant of second-order conditioning to combat the problem of conditioning a subconscious stimulus. Subjects were exposed to 2 Hz magnetic field intensity oscillations as the CS, which was paired with an auditory stimulus and followed by a shock. Initially, both stimuli were presented together, with the auditory stimulus serving as a conscious CS1 and the magnetic field as a subconscious CS2. As the experiments progressed, the auditory stimulus was gradually faded out, leaving the magnetic field to elicit the conditioned response independently. This approach did show CRs to occur when presented with the magnetic field alone with  $p \leq 0.01$ . However, due to technical limitations, the study was never published. Our experiment seeks to replicate this method of first pairing the magnetic cue with an auditory cue, after which we gradually fade out the auditory cue. However, we use magnetic field rotations instead of oscillating intensity, as only rotations have been shown to elicit a neural response [\(Wang](#page-60-0) [et al., 2019b\)](#page-60-0). While intensity oscillations might also provoke responses, this remains untested, and we chose to begin with rotations based on the existing evidence.

### <span id="page-23-2"></span>4.2.2 Methods

#### 4.2.2.1 Stimuli and Procedure

In this experiment, the conditioned stimulus (CS) was the rotation of the Earth's magnetic field, the unconditioned stimulus (US) was an electric shock, and the conditioned response (CR) was electrodermal activity (EDA). The experiment was conducted inside the radio frequency-shielded chamber, as described in Section [2.3.](#page-10-3) The magnetic field's declination was rotated between northwest (NW) and northeast (NE) directions (-45° to 45°) over 4000 milliseconds. The inter-trial interval (ITI) was between 11000 and 26000 milliseconds. During trials with an auditory stimulus (A), the sound played simultaneously with the magnetic field rotation and ended at the same time (lasting 4000 milliseconds). The experimenter manually adjusted the speaker volume between trials. The US was delivered during the last 100 milliseconds of the magnetic field rotation. Technical details of the shock circuit can be found in Appendix [B.](#page-52-0) A schematic timeline of a single trial can be found in Figure [4.1.](#page-24-1)

The experimental design employed an  $n=1$ 

<span id="page-24-1"></span>

**Figure 4.1:** Schematic timeline of a single trial  $\text{CS} = \text{Conditional Stimulus}$ ,  $\text{US} = \text{Unconditioned Stimulus}$ , ITI = Intertrial Interval).

within-subject approach, consisting of 15 trials, including the habituation phase. The selection of a relatively low number of trials was informed by observations from initial pilot testing, which indicated rapid habituation to the US. To address the potential for a blocking effect during the learning phase, where prior learning of an association between stimulus A and the US  $(A \rightarrow US)$  can overshadow subsequent learning of an association between a compound stimulus A+B and the US  $(A+B\rightarrow US)$ , we commenced the conditioning with the simultaneous presentation of both stimulus A (the magnetic stimulus) and stimulus B (the auditory stimulus). Given the unconscious nature of the CS, the fixed trials served as a comparison between a non-predictor of the US (i.e. fixed magnetic field) and a predictor of the US (i.e. magnetic field rotation).

Participants were seated comfortably in the chamber, having removed all magnetic or electronic devices. They were instructed to keep their eyes closed and to remain still throughout the experiment. The experiment comprised three phases: pre-acquisition, conditioning, and fading. See Table [4.1](#page-25-0) for an overview of the utilized trial structure. Each block of trials was followed by a short break. Note that a extinction phase was omitted due to our focus on the possibility of effective acquisition, as well as lack of relevance of extinction to our research question.

- In the pre-acquisition phase, the US intensity was calibrated to ensure that it was aversive but not overly painful. The participant adjusted the shock level between 0-3 mA and then underwent a habituation phase with three trials of the auditory stimulus at full volume (AH) to establish baseline EDA measurements.
- The conditioning phase included two blocks, each with three trials. During each trial, the

CS & audio (AH) was paired with the US with a 100% reinforcement rate.

• Finally, in the fading phase, the volume of the auditory stimulus was gradually decreased in a pseudo-random fashion, while the aversive conditioning with the US was maintained. The last trial did not include the US. The experimenter randomly determined the number of trials in this phase to prevent the participant, who is also an author of the study, from anticipating the cessation of the US, which could introduce cognitive biases and affect the EDA measurements.

#### 4.2.2.2 Data Collection

EDA was recorded using the Biopac MP160 system with an EBI100C Electrobioimpedance Amplifier with Ag/AgCl electrodes attached to the participant's non-dominant hand. The data was sampled at 1000 Hz and filtered with a 1 Hz low-pass filter to remove noise. The shocks were controlled using an Arduino Uno R4 Minima, which received event triggers at the onset of the magnetic field rotations to time the auditory stimulus and US accordingly. The auditory stimulus was delivered via a set of calibrated speakers.

#### <span id="page-24-0"></span>4.2.3 Results

Due to time constraints and the absence of a detectable conditioned response (CR), no further statistical analysis was performed. Additionally, technical issues occasionally caused the trial trigger to activate without an actual trial, complicating statistical analysis even further. Examples of electrodermal activity (EDA) responses are shown in Figure [4.3.](#page-26-0)



(a) Shock Control Box including a shock level dial (0-3mA) and test trigger.



(b) EDA was measured using the BioPac MP160 system.



(c) The experimental setup with the subject connected to both the EDA measuring equipment on the non-dominant hand and the shock delivery system on the right hand.

<span id="page-25-0"></span>Figure 4.2: Additional images of aspects of the experimental setup

Phase	<b>Block</b>	Trial	Stimuli
Habituation	∩	1	AH
		$\overline{2}$	ΑH
		3	AH
Conditioning	1	4	CS & AH & US
		5	$CS \& AH \& US$
		6	$\overline{\text{CS}}\ \&\ \text{AH}\ \&\ \text{US}$
	$\overline{2}$		CS & AH & US
		8	$CS \& AH \& US$
		9	$\overline{\text{CS}}$ & AH & US
Fading	$\overline{4}$	10	CS & AH & US
		11	CS & AM & US
		12	CS & AL & US
		13	$CS \& AL \& US$
		14	CS & US
		15	CS

Table 4.1: Trial structure of the Pavlovian conditioning experiment. CS: Conditioned Stimulus, US: Unconditioned Stimulus, AH: Audio High, AM: Audio Medium, AL: Audio Low

<span id="page-26-0"></span>

(a) Electrodermal Activity (EDA) response during the magnetic field rotation (conditioned stimulus, CS) paired with high-intensity audio (AH) and followed by an electric shock (unconditioned stimulus, US). This represents the CS & AH & US condition, showing the participant's physiological response to the compounded stimuli.



(b) Electrodermal Activity (EDA) response to magnetic field rotation (CS) without audio, followed by an electric shock (US). This CS & US condition highlights the participant's physiological response to the magnetic stimulus in the absence of auditory cues.



(c) Electrodermal Activity (EDA) response to magnetic field rotation (CS) without accompanying audio or electric shock. This CS-only condition illustrates the baseline physiological response to the magnetic stimulus alone.

Figure 4.3: Three examples of EDA activity across different experimental conditions. The red line denotes the stimulus trigger, with low values indicating active states (e.g., magnetic field rotation, audio on). The EDA signal is represented by the pink line.

### <span id="page-27-0"></span>4.2.4 Discussion

In this pilot experiment, we encountered several technical and design limitations that likely contributed to the lack of success. Firstly, the number of trials may have been insufficient to establish a significant conditioning effect with the magnetic stimuli. Additionally, the electrodermal activity (EDA) response exhibited a delayed onset, making it difficult to determine whether changes were initiated by the magnetic field rotation or were simply reactions to the subsequent shock. This temporal ambiguity complicates the interpretation of causality between the stimuli and the physiological response. Furthermore, as both the primary author and the subject of the experiment, I may have become habituated to the audio stimulus, potentially reducing its effectiveness as a novel conditioned stimulus. My prior knowledge of the trial structure may have introduced bias, influencing my responses. Another concern is the possibility of blocking or overshadowing effects, where the association between the audio cue and the shock was learned quickly, overshadowing the intended conditioning of the magnetic stimulus. This overshadowing may have prevented the establishment of a reliable association between magnetoreception and the unconditioned stimulus, ultimately impacting the experiment's overall results.

Moreover, the nature of magnetoreception itself may pose fundamental challenges to classical conditioning paradigms. Conditioning experiments using magnetic stimuli have largely been unsuccessful, with only rare successes. As reviewed by [Wiltschko and Wiltschko](#page-60-6) [\(1996\)](#page-60-6), conditioning EMF cues is particularly challenging because these cues do not undergo the rapid changes that are typically needed for effective conditioning. Magnetic cues rarely directly relate to fear or immediate reactions, making latent connections difficult to establish. Additionally, the Earth's magnetic field primarily changes due to the animal's movements rather than external changes, leading to potential neglect of these cues except in navigation contexts.

### <span id="page-27-1"></span>4.2.5 Conclusion

Given the inherent difficulties of conditioning magnetic stimuli, this pilot experiment suggests that a classical conditioning paradigm may not be the most appropriate approach for studying human magnetoreception. The challenges we identified, both technical and conceptual, indicate that alternative methods may be needed. A promising future direction would be to adopt a directional training paradigm, such as training participants to navigate a maze in a specific magnetic direction within a virtual reality environment. By manipulating the direction within the experimental chamber, participants could be prevented from cognitively realizing the consistent exit location, potentially leading to more effective conditioning. This proposed experiment, however, requires further consideration and refinement before implementation.

### <span id="page-28-0"></span>4.3 Experiment 4: Enhancing Magnetoreception Through Sensory Substitution

Abstract. We explored human magnetoreception using the MESSy headband, a sensory substitution device that converts Earth's Magnetic Field (EMF) changes into haptic feedback. A single participant  $(n=1)$  underwent a onehour training session in a controlled magnetic environment. EEG recordings and behavioral tasks before and after training were used to assess changes. Posttraining EEG results showed neural activity changes, suggesting possible neural plasticity related to magnetosensory processing. A subtle shift in visual motion perception hinted at some reweighed integration between vision and magnetoreception. While these results are promising, longer and more behaviorally relevant training sessions are likely needed to enhance human magnetoreception.

### <span id="page-28-1"></span>4.3.1 Introduction

Returning to the key idea that human magnetoreception might be a vestigial sense that could be relearned, sensory substitution (SS) offers a promising approach for testing this hypothesis. Sensory substitution involves conveying information typically mediated by one sense through another and is usually utilized to substitute for a damaged sense. In certain cases, the effects of the sensory substitution device can be retained even after removing the device. This retention effect testifies to its potential to reorganize the sensory cortex and is relevant to our aim of enhancing human magnetoreception.

### 4.3.1.1 Sensory Substitution

The concept was first demonstrated by [Bach-Y-](#page-56-7)[Rita et al.](#page-56-7) [\(1969\)](#page-56-7), who transformed a camera's video feed into vibrotactile stimuli on the skin of blind subjects. After some practice, these subjects could identify objects in front of the camera by feeling vibrations on their skin. This demonstrates the brain's ability to interpret alternative sensory mappings, suggesting that cortical regions responsible for specific sensory modalities might not be as specialized as traditionally believed, a conclusion that multiple lines of work converged to [\(Ghazanfar and](#page-57-10) [Schroeder, 2006;](#page-57-10) [Shimojo, 2001\)](#page-59-7). Since then, numerous proofs-of-concept have shown the substitution of one sensory modality for another, such as deaf patients learning to "hear" through tactile sensations [\(Novich and Eagleman, 2015\)](#page-58-11) and blind individuals learning to "see" using auditory stimulations [\(Ward and Meijer, 2010;](#page-60-4) [Stiles and](#page-59-8) [Shimojo, 2015\)](#page-59-8).

### 4.3.1.2 Retention of Changes Induced by Sensory Substitution

Strikingly, some sensory substitution devices have effects that outlast their use. [Tyler et al.](#page-59-9) [\(2003\)](#page-59-9) provided patients with vestibular dysfunction—a condition impairing their ability to balance while standing or sitting due to vestibular system damage—with a device worn on their tongue. This device, known as the "BrainPort balance device," featured a grid of 12 x 12 electro-tactile stimulators that conveyed head tilt information (see Figure [4.4\)](#page-29-0). Within minutes, many patients who had been unable to balance for years were now able to do so, integrating the device's information into their vestibular system. Remarkably, subjects experienced a residual effect: after using the device for 10 minutes, they could maintain balance for an additional 10 minutes without it. Moreover, with longer training sessions, the residual benefits were extended, in one case persisting for up to 8 weeks beyond the training period.

The underlying mechanism for this retention of vestibular improvement is not fully understood, but the prevailing theory suggests that the Brain-Port device closes an otherwise open-loop control process [\(Tyler et al., 2003;](#page-59-9) [Bach-y Rita et al.,](#page-56-8) [2005b;](#page-56-8) [Danilov et al., 2008;](#page-56-9) [Wall and Kentala,](#page-59-10) [2010;](#page-59-10) [Sienko et al., 2018,](#page-59-11) [2017\)](#page-59-12). Normally, sensory data from the vestibular, visual, tactile, and proprioceptive systems are integrated into a sensorimotor closed-loop control system driving effective body movement and balance. In the absence of normal vestibular or other input, the intrinsically unstable system becomes vulnerable to internal and external noise. The BrainPort device is thought to provide the missing information necessary for effective multisensory integration while also enabling the central nervous system to reweigh its sensory inputs, allowing the system to remain stable even after the device is removed.

The story of the BrainPort balance device is highly relevant to our investigation of the plasticity of magnetoreception. The BrainPort's ability to induce lasting improvements in vestibular function through consistent use demonstrates the potential for sensory substitution devices to create persistent neural adaptations. Drawing on this, our re-

<span id="page-29-0"></span>

(a) The effects of wearing the BrainPort vestibular substitution device. The device is embedded in a helmet (top-left), which hosts an electrotactile tongue interface (top-right). The graphs show head position as a function of time (y-axis), with and without the BrainPort. Sourced from [Bach-y](#page-56-10) [Rita et al.](#page-56-10) [\(2005a\)](#page-56-10).



(b) Retention of rehabilitation effects from shortterm vestibular substitution (VS) training is shown. In each row, the left half represents performance with the BrainPort device, while the right half shows performance without it. Instability typically emerged in the non-VS period after 30% of the VS training duration. Sourced from [Tyler et al.](#page-59-9) [\(2003\)](#page-59-9).

Figure 4.4: (a) Effects of wearing the BrainPort device and (b) retention of rehabilitation effects from shortterm VS training.

search hypothesizes that a magnetosensory substitution (MSS) device—designed to convey magnetoreceptive information through an alternative sensory modality—can similarly train individuals to develop magnetoreception by associating the consciously perceived sensory input from the MSS device with the neural vestiges of magnetoreception. The residual effects observed with the BrainPort suggest that the central nervous system can integrate and utilize new sensory inputs to reweigh and compensate for damaged sensory systems, retaining changes in these networks. Given our premise that the neural signature for magnetoreception in humans (alpha-ERD, see [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0)) represents vestiges of an underdeveloped sense, we hypothesize that such residual effects could also be observed after MSS training.

#### 4.3.1.3 North-Substituting Devices

The task, therefore, is to create a sensory substitution device that mediates the Earth's Magnetic Field (EMF). Since [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) demonstrated that humans only show a neural response to changes in the declination of the EMF, we chose to omit the mediation of other properties of the EMF, such as inclination or intensity, which are detectable by other animals. Fortunately, we can draw from sensory substitution studies for enhancing navigation. Numerous studies have investigated devices that mediate a sense of North [\(Nagel](#page-58-12) [et al., 2005b;](#page-58-12) [Kaspar et al., 2014b;](#page-57-11) [Schumann and](#page-59-13) [O'Regan, 2017b;](#page-59-13) [Witzel et al., 2023\)](#page-60-7). The pioneering study by [Nagel et al.](#page-58-12) [\(2005b\)](#page-58-12) utilized a belt equipped with thirteen vibratory motors, with the motor pointing North vibrating continuously. Other studies by [Witzel et al.](#page-60-7) [\(2023\)](#page-60-7); [Schumann](#page-59-13) [and O'Regan](#page-59-13) [\(2017b\)](#page-59-13) translated cardinal directions into auditory cues delivered through headphones. However, all these studies (see Table [4.2](#page-31-0) for an overview) either preceded or seemingly overlooked the findings of [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0), which demonstrated that humans can transduce Earth's magnetic field. Therefore, they attributed any improvements in navigational or spatial abilities to general training rather than to an inherent magnetoreceptive capability.

We posit that the improvements observed in subjects from previous experiments, particularly those involving longer-term training, may be attributable to the development of actual magnetoreception. This could occur through either the closing of the sensorimotor feedback loop between self-movement and sensory input or through increased attentional focus on this potential sense. Notably, these subjective "spatial sense" or "stability" enhancements were more pronounced with extended training durations and when the training involved outdoor activities across large distances, such as biking or hiking. Additionally, [Nagel et al.](#page-58-12) [\(2005b\)](#page-58-12) highlighted the importance of motivation and wearing comfort, factors that will be prioritized in the design of our wearable device.

#### 4.3.1.4 Hypothesis

We propose that training with a magnetosensory substitution (MSS) system might enhance true magnetoreception by leveraging sensory plasticity, thereby offering a unique opportunity to explore both the mechanisms of neural adaptation and the manifestation of new sensory experiences (qualia). To test this hypothesis, we developed a prototype MSS device and conducted a controlled pilot experiment, where the participant underwent a one-hour training session. The effectiveness of this training is evaluated by comparing pre- and post-training measurements, focusing on behavioral tasks (described in Stimuli and Procedure), as well as lowlevel neural responses to geomagnetic stimuli measured via EEG. Although we hypothesize that extended use of the MSS device over months, particularly in a mobile lifestyle, could foster the development of true magnetoreception, this pilot experiment is designed to identify which measurements are most indicative of progress, if any. By assessing the impact of short-term training, we aim to determine which metrics will be valuable for evaluating success in future long-term studies.

#### 4.3.1.5 The MESSy headband

We have developed a haptic device, the Magnetoreception Enhancing Sensory Substitution (MESSy), that is responsive to cardinal directions. The device, worn as a portable headband (see Figure [4.5\)](#page-32-0), utilizes a small compass sensor to track the wearer's location in space and then translates that information into a vibration pattern around the user's head (see Figure [4.6](#page-33-0) for an illustration of the mapping logic). Subjectively, the wearer becomes aware of which direction is north, relative to their head position. We chose head-based tactile feedback because (i) it provides intuitive, 360° directional information without interfering with vision or hearing, (ii) aligns with the hypothesized location of magnetoreceptive mechanisms in the brain, and (iii) integrates seamlessly with other senses, thereby increasing multisensory interaction and intuitiveness. The current design uses a Teensy<sup>™</sup> 4.0 attached to a 9-axis IMU sensor (MPU-9250), powered by a 3.7V LiPo battery, connected over I²C to thirteen motors (LS-00046), each driven by a haptic driver (DRV2605L), which is incorporated into a headband made out of felt. Leveraging a wellknown haptic illusion [\(Alles, 1970;](#page-56-11) [Rahal et al.,](#page-58-13) [2009\)](#page-58-13), the wearer can experience tactile stimulation in illusory locations anywhere between two vibrating motors. This gives the impression of smooth motion across the axis of the headband as the wearer rotates in space. For a detailed description of the MESSy headband, including its design considerations, components, and algorithm, please refer to Appendix [A.](#page-46-0)

### <span id="page-30-0"></span>4.3.2 Methods

#### 4.3.2.1 Equipment

#### 4.3.2.1.1 Magnetic field manipulation

The experimental setup for the magnetic field manipulation is described in Section [2.3.](#page-10-3) The same modular, portable, radio frequency-shielded chamber was used.

#### 4.3.2.1.2 MESSy headband details

The Magnetoreception Enhancing Sensory Substitution (MESSy) headband as described in Appendix [A](#page-46-0) was used.

#### 4.3.2.2 Stimuli and Procedure

The experiment employs a within-subjects design with a single participant  $(n=1)$  to evaluate various measurements before and after a defined training period. As a pilot study, the training duration was limited to one hour within the magnetic field manipulation chamber while the participant wore the Magnetoreception Enhancing Sensory Substitution (MESSy) headband. This design choice is supported by prior research on cross-modal plasticity, such as the study by [Merabet et al.](#page-58-14) [\(2007\)](#page-58-14), which found that blindfolded participants engaged in a tactile discrimination task exhibited activity in the primary visual cortex after just forty to sixty minutes. The training session included 1000 trials, divided into 5 blocks of 200 trials each. The independent variable in this experiment is the training condition, with measurements taken (without wearing the MESSy headband) both before and after the training session. The dependent variables include EEG recordings and several behavioral tasks: the left-right detection task, a spatial orientation task, and the visual motion detection task detailed in Section [3.3.](#page-18-0)

The experimental procedure is divided into three main phases: pre-training measurements, training, and post-training measurements. During the onehour training session, the participant was exposed to randomized EMF rotations, with the MESSy

<span id="page-31-0"></span>

Table 4.2: Literature overview of North-translating sensory substitution studies, in chronological order.

<span id="page-32-0"></span>

Figure 4.5: Features of the MESSy headband

<span id="page-33-0"></span>

Figure 4.6: Illustration of the MESSy device giving cardinal direction information through vibrotactile stimulations. The amplitude of the vibration is denoted with the saturation of the color.

headband providing real-time haptic feedback. To control for potential order effects, the sequence of tasks within each measurement session was randomized.

- In the training phase of the magnetosensory substitution experiment, the magnetic field's declination was rotated between northeast (NE) and southeast (SE) directions (45° to 135°) while maintaining a downward inclination of +60°. These rotations occurred over 100 milliseconds every 3.6 seconds. The MESSy headband, worn by the participant, successfully recognized the manipulated North as North, providing a corresponding moving vibrotactile feedback as the magnetic field changed. The MESSy headband was not RFshielded as described earlier, since the copper fabric shield introduced unstable functioning, possibly due to accidental shorting. To overshadow the introduced auditory artifact from the vibrotactile motors, Brownian noise was played on speakers positioned outside of the cage.
- In the left-right detection task, the participant was seated inside the chamber with eyes closed while the EMF rotated between NE and SE (45° and 135°). After each rotation, an auditory cue signaled the participant to provide feedback via a button box, with two buttons corresponding to left and right. Once feedback was provided, the next trial commenced. A total of 200 trials were conducted (100 pretraining and 100 post-training), with the direction of the magnetic field randomized to

prevent any biases.

- The visual motion detection task followed the procedure detailed in Section [3.3.](#page-18-0) The task consisted of 150 trials before and after training (50 right rotation, 50 left rotation, and 50 fixed trials randomly intermixed), totaling 300 trials.
- In the spatial orientation task, the participant, seated blindfolded in a rotating chair, was manually rotated by the experimenter. To eliminate potential auditory or visual cues regarding orientation, the experiment was conducted in a quiet environment, and the experimenter moved around the participant randomly to prevent them from deducing their orientation based on the experimenter's position. After the rotation, the participant was asked to point toward North using a stick with an attached smartphone running a compass app. The long stick was chosen to reduce pointing ambiguity, as holding the phone alone could result in subtle, involuntary wrist rotations that might interfere with measurement accuracy. Using both arms to handle the stick made the participant's intended direction more pronounced and less prone to error.
- EEG data collection followed a similar procedure as in [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0). Continuous EEG was recorded from 64 electrodes using a BioSemi Active Two System. Two horizontal electrooculogram electrodes were placed adjacent to the outer canthi and were used to

record horizontal eye movements. A vertical electrooculogram electrode was placed beneath the right eye and used to record eyeblinks and vertical eye movements. To maximize data quality, impedances were reduced to less than 20 k $\Omega$  for the scalp electrodes and EOG electrodes.

#### 4.3.2.3 EEG Data Analysis

Offline analysis was performed using EEGLAB [\(Delorme and Makeig, 2004\)](#page-56-4) and ERPLAB [\(Lopez-](#page-58-8)[Calderon and Luck, 2014\)](#page-58-8). Data were resampled at 250 Hz. A noncausal Butterworth bandpass filter was applied (half-amplitude cutoffs = 0.1 Hz and 80 Hz, slope  $= 12$  dB/octave), and all channels were re-referenced offline to channel P9. Independent component analysis (ICA) was used to correct for eye blinks and eye movements in the continuous EEG data. Stimulus-locked ERPs were generated using an epoch of -750 to 2000 ms.

Analysis was replicated from [Wang et al.](#page-60-0)  $(2019b)$ . The baseline interval was from  $-500$ 250 ms prestimulus. Time/frequency decomposition was performed for each trial using Fast Fourier Transform (MATLAB function  $\{f(t(x))\}$  and Morlet wavelet convolution on 100 linearly spaced frequencies between 1 and 100 Hz. Average power in an extended alpha-band of 6–14 Hz was computed for the pre-stimulus and post-stimulus intervals of all trials, and a threshold of 1.5 times the interquartile range was applied to identify trials with extreme values of log alpha-power. These trials were excluded from further analysis but retained in the data. After automated trial rejection, ERPs were computed for each condition and then subtracted from each trial of that condition to reduce the electrical induction artifact that appeared only during the 100-ms magnetic stimulation interval. This removes phase-locked components from an EEG signal for subsequent analysis of non-phase-locked, time/ frequency power. Non-phase-locked power was computed at midline frontal electrode Fz for each trial and then averaged and baseline-normalized for each condition to generate a time/frequency map from 250 ms pre-stimulus to 2000 ms post-stimulus and 1–100 Hz. To provide an estimate of overall alpha power, power spectral density was computed using Welch's method (MATLAB function pwelch $(x)$ ) at 0.5-Hz frequency resolution [\(Welch, 1967\)](#page-60-9).

#### <span id="page-34-0"></span>4.3.3 Results

### 4.3.3.1 Behavioral Task Results

### 4.3.3.1.1 Left-Right Detection Task

Before and after MSS training, the participant undertook a decision task (without wearing the MESSy headband) requiring them to guess whether magnetic North was to their left or right. Contrary to expectations, the results indicate a significant decline in performance following the training. The participant's pre-training responses aligned more closely with the magnetic field direction, with a correct response rate of 60%. However, this rate dropped to 48% after training (see Figure [4.7\)](#page-35-0). A statistical analysis using a two-proportion z-test revealed that this decrease in performance is significant ( $z = 2.41$ ,  $p = 0.016$ ), suggesting that the training may have adversely affected the participant's ability to correctly identify the direction of magnetic North.

### 4.3.3.1.2 Visual Motion Detection Results

The participant completed a visual motion detection task as outlined in Section [3.3](#page-18-0) both before and after the training period. The performance was measured in terms of the proportion of responses congruent with the magnetic field rotation at two different levels of visual coherence, 0% and 60%, with 150 trials conducted in both the pre-training and post-training sessions (50 right rotation, 50 left rotation, and 50 fixed trials randomly intermixed).

Figure [4.8](#page-35-1) summarizes the proportions of congruent and incongruent responses observed before and after the training at 60% and 0% coherence levels.

At 0% coherence, the proportion of congruent responses increased marginally from 0.49 pretraining to 0.51 post-training. At 60% coherence, however, the proportion of congruent responses showed a more substantial increase from 0.44 pretraining to 0.55 post-training. A statistical analysis using a two-proportion z-test for paired data revealed that this increase at 60% coherence is significant ( $z = 2.69$ ,  $p = 0.007$ ), indicating a significant change in visual motion perception following the training.

#### 4.3.3.1.3 Spatial Orientation Results

The participant completed a spatial orientation task consisting of 10 trials before and after the training period, resulting in 20 trials. Figure [4.9](#page-37-0)

<span id="page-35-0"></span>

<span id="page-35-1"></span>

Figure 4.7: Results for left-right detection task -Responses before and after magnetosensory training. In the top figure, the proportion of responses congruent with the magnetic field rotation direction is illustrated. In the bottom figure, the proportion of left vs right responses is illustrated.

Figure 4.8: Results for visual motion detection task — Proportions of responses congruent and incongruent to the magnetic field rotation before and after MSS training at 0% (top figure) and 60% (bottom figure) coherence levels.

shows no significant difference in pointing accuracy between the pre-training and post-training sessions.

To assess training effectiveness regarding directional data, we fitted the von Mises distribution (i.e. a normal distribution for circular data) to the pre-training and post-training data. The analysis revealed that the mean direction  $(\mu)$  of guesses before training was 340.86°, with a concentration parameter  $(\kappa)$  of 1.0. Following training, the mean direction shifted to 259.22°, with the concentration parameter remaining at 1.0.

These results suggest that training did not lead to an improvement in the accuracy of directional guesses. The shift in mean direction did not move the guesses closer to the true North  $(0^{\circ}/360^{\circ})$ , and the concentration of guesses around the mean direction remained unchanged. Consequently, the training did not enhance participants' spatial orientation in the context of this task.

#### 4.3.3.2 EEG Results

Preliminary results (Figure [4.10](#page-38-0) and Figure [4.11\)](#page-39-0) showed that in the pre-training condition (before wearing the MESSy headband), we replicated the results found in [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0). We found a decrease in EEG alpha-power (i.e. alpha-ERD) in response to counterclockwise magnetic field rotations relative to the clockwise and fixed conditions. In the post-training condition, which involved the participant sitting in the chamber with the headset and becoming accustomed to feeling the MESSy headband's vibrotactile feedback in response to the magnetic field rotation (1,000 trials) in the cage, we found that the pattern shifted. In the posttraining condition, the results showed that alpha power evened out across conditions. The decrease in EEG alpha-power was greatest in the clockwise relative to the counterclockwise and fixed conditions.

#### <span id="page-36-0"></span>4.3.4 Discussion

Unfortunately, during the MSS training, the MESSy headband was not RF-shielded, as the copper fabric shield caused instability, possibly due to shorting. Thus, we cannot exclude the possibility that RF noise affected magnetoreception, leading to the lack of improvement in behavioral or EEG measurements. Furthermore, the magnetic effects of the motors can also not be excluded as an inhibiting factor. However, the participant, who also developed the headband, wore it daily during development. Thus, if RF or magnetic noise had impaired magnetoreception, it would likely have disrupted the EEG consistently, both before and after training. Therefore, any difference in sensitivity post-training remains significant. Alternatively, if RF or magnetic noise only briefly inhibits magnetoreception, the EEG measurements could be diluted.

### 4.3.4.1 Behavioral Task Performance

#### 4.3.4.1.1 Left-Right Detection Performance

We observed a reduction in congruency with the magnetic field direction, approaching chance levels (Figure [4.7\)](#page-35-0). This may be attributed to the RF interference caused by the unshielded MESSy headband. In retrospect, a more appropriate behavioral measure might have been to determine whether a change in the geomagnetic field occurred, as the neural response identified by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0) was linked to changes in the magnetic field rather than to its absolute position. Consequently, the MESSy headband may be more likely to associate neurally with change detection rather than with absolute position detection (left vs right).

### 4.3.4.1.2 Visual Motion Detection Performance

Firstly, it is important to note that all results hover around chance level, so any interpretation remains speculative.

In the 0% coherence condition, performance remained at chance level. However, in the 60% coherence condition, visual motion perception appeared to be marginally influenced by geomagnetic information. Prior to training, there was a bias towards responses that were incongruent with the magnetic field rotation direction. Post-training, this bias was reversed, with a greater number of responses aligning with the magnetic field rotation direction.

Interpreting this shift towards greater congruency with the magnetic field rotation direction is challenging. This increase in congruence might suggest an improvement, but it could also be inconsequential. One possibility is that the MSS training successfully associated the haptic feedback with magnetoreception, leading to increased congruency as  $-$  during the post-training measurement without the MESSy headband — the brain linked changes in the magnetic field with tactile phantom sensations. This could result in an arbitrary relationship with visual motion perception, akin to how arbitrary connections such as natural

<span id="page-37-0"></span>

Figure 4.9: Results from the spatial orientation task visualized in a circular graph. No difference is visible between pre- and post-training.

language and audio pitch can influence visual motion perception [\(Sadaghiani et al., 2009\)](#page-59-5). The pretraining measurements might reflect more ecologically relevant connections, as discussed in Section [3.3.](#page-18-0) In further unpublished tests by [Krisst et al.](#page-57-7) [\(2024\)](#page-57-7) with additional participants  $(n=13)$ , the dominant pattern observed was participants perceiving visual motion in opposition to the magnetic field rotation direction. Thus, MS training appears to have influenced the sensory integration of magnetoreception and vision, as these post-training results show the highest congruency among the 13 participants tested.

#### 4.3.4.1.3 Spatial Orientation Performance

The spatial orientation task showed no significant difference between pre- and post-training (Figure [4.9\)](#page-37-0), with both performances at chance level. This may be attributed to the limited number of trials (10 pre, 10 post), but it is also possible that the spatial orientation task is a behavior too complex to be affected by a brief period of MSS training.

#### 4.3.4.2 Neural Correlates

The uncertainty surrounding the role of alpha event-related desynchronization (alpha-ERD) in this context prevents us from definitively determining whether the observed neural changes reflect progress toward enhanced magnetoreception or simply represent a non-specific response to novel stimulation. Another point of discussion is the selective response to clockwise versus counterclockwise magnetic field rotations, which echo the findings by [Wang et al.](#page-60-0) [\(2019b\)](#page-60-0). As suggested by [Wang](#page-60-0) [et al.](#page-60-0) [\(2019b\)](#page-60-0), this selectivity could arise from the chirality of biological structures involved in magnetoreception, which may favor the transduction of one type of stimulus over its opposite. Alternatively, higher-level cognitive processes could bias the neural response toward counterclockwise rotations, independent of any asymmetry at the receptor level. The selectivity might also be an evolutionary by-product or serve as a mechanism for detecting geomagnetic anomalies, providing warnings about sudden shifts in the magnetic field.

Although we lack concrete evidence, we propose an additional speculative hypothesis for consideration in future research: perhaps a response to only one direction of rotation may be sufficient for the neural computations required to estimate self-orientation. This could involve the integration of vestibular and magnetoreceptive information, where physical rotations in one direction trigger a specific pattern of vestibular and magnetoreceptive firing, while rotations in the opposite direction trigger solely vestibular input without corresponding magnetoreceptive activation.

Regardless of the specific interpretation of alpha-ERD and response selectivity, future MSS studies could treat these phenomena as a black box and focus instead on comparing neural sensitivity before and after training. This comparison should involve two types of within-subject measurements,



<span id="page-38-0"></span>

(a) Pre-training EEG results. A decrease in EEG alpha-power in the counterclockwise (CCW) condition was found, replicating results found by [Wang](#page-60-0) [et al.](#page-60-0) [\(2019b\)](#page-60-0).



(b) Post-training EEG results. A decrease in EEG alpha-power in the clockwise (CW) condition was found and attenuation of the counterclockwise (CCW) alpha-power decrease.

Figure 4.10: EEG results show a difference in geomagnetic sensitivity between pre-training (a) and posttraining (b).

one with training and one without, and should include a control condition where the MESSy headband is worn without providing accurate neural feedback, but only exposes the subject to the same RF and magnetic noise. This approach could help clarify whether training influences neural sensitivity in a meaningful way.

### 4.3.4.3 On Magnetosensory Substitution

The one-hour magnetosensory substitution (MSS) training session with the MESSy headband provided some intriguing, albeit inconclusive, insights. Our EEG measurements suggest that there was a detectable change in neural activity following the training. However, the nature of this change—whether it represents an enhancement or degradation of magnetoreceptive ability—remains uncertain. The ambiguity surrounding the function of alpha event-related desynchronization (alpha-ERD) in this context leaves us unable to conclusively interpret whether these neural changes indicate progress toward enhanced magnetoreception or simply a non-specific neural response to novel stimulation.

When we consider the behavioral outcomes, such as the visual motion detection task, we observed some changes post-training. These changes might hint at the brain beginning to form associations with magnetic cues and integrating them into visual processing. The observed alterations could reflect short-term neural adjustments—perhaps the unmasking of previously inactive connections—but we lack sufficient evidence to confirm that these are specific to magnetoreception or that they represent meaningful progress.

The more complex behavioral tasks, like determining the geomagnetic field's orientation or pointing North, did not show significant improvement. This lack of change might suggest that these tasks require a level of cortical remodeling that was beyond the scope of our brief training session. It's plausible that more extensive and prolonged training could induce the slower, structural changes necessary for such high-level behaviors, but this hypothesis remains to be tested.

It should also be considered that the training in this pilot experiment did not reflect training in a biologically meaningful approach. In other words, the experimental stationary setting might not induce the recruitment of geomagnetic information as would happen in an orientation-related task. Described as the modality appropriateness hypothesis [\(Welch and Warren, 1980\)](#page-60-10), the brain appears to combine different sensory cues by weighting

<span id="page-39-0"></span>

Figure 4.11: Time-frequency plots showing EEG power spectra for three conditions: counterclockwise (CCW) trials, clockwise (CW) trials, and fixed trials before (left) and after (right) training at electrode Fz. The y-axis represents frequency (Hz), and the x-axis represents time (seconds) relative to stimulus onset (at 0 seconds). Black vertical lines indicate the 0- to 100-ms magnetic field rotation period. Warmer colors indicate higher power, while cooler colors indicate lower power. Post-stimulus power changes (dB) from a pre-stimulus baseline (-500 to -250 ms) are plotted according to the -4-dB color bar on the right. Alpha-ERD as a response to magnetic field rotation can be seen between the 6-14 Hz range in the pre-training CCW condition (dark blue) at 500 ms after the field sweep. This response is attenuated after training.

them based on the appropriateness for the task at hand. For example, in the case of the aforementioned vestibular substitution experiment [\(Bach-y](#page-56-8) [Rita et al., 2005b\)](#page-56-8), the task of attempting to balance might force the brain to integrate the information from the vestibular substitution device more actively as it is highly relevant for the objective.

### <span id="page-40-0"></span>4.3.5 Conclusion

This pilot experiment exposed several challenges and limitations that likely contributed to the inconclusive results. Although changes in neural activity and behavioral responses were noted following magnetosensory substitution (MSS) training, these changes were difficult to interpret due to confounding factors such as RF and magnetic noise, the short duration of training, and the small sample size. The selective response to magnetic field rotations and the ambiguous role of alpha-ERD add further complexity to the findings, underscoring the need for more robust experimental designs in future research. Moving forward, incorporating control conditions—such as training without the MESSy headband and using a compromised MESSy headband during training—will be essential to clarify the differences in neural sensitivity observed after MSS training. Addressing RF noise and magnetic interference, possibly through a revised design of the MESSy headband, will also be critical. Additionally, refining the training protocols to include more biologically meaningful tasks and extending the training duration with a larger sample size will be necessary to obtain more definitive results.

## Chapter 5

# **Conclusions**

### <span id="page-42-0"></span>5.1 Summary

Chapter [1](#page-6-0) provided a high-level overview of the topic, setting the stage for exploring human magnetoreception and its potential trainability.

Chapter [2](#page-10-0) introduced concepts and general experimental details relevant to the following experiments.

Chapter [3](#page-12-0) investigated whether human magnetoreception is integrated with other senses, focusing on the vestibular and visual systems. In pilot experiment 1, we tested whether the vestibuloocular reflex is influenced by magnetoreception. In pilot experiment 2, we explored the impact of magnetoreception on visual motion perception.

Chapter [4](#page-22-0) explored methods to enhance human magnetoreception through conditioning and sensory substitution, testing their efficacy in inducing neural associations with magnetic stimuli. In pilot experiment 3, we tested whether aversive conditioning could produce a conditioned response to the geomagnetic field. In pilot experiment 4, we evaluated whether a 1-hour magnetosensory substitution training session could induce behavioral and neural changes.

### <span id="page-42-1"></span>5.2 Integrated Discussion

We investigated the potential to enhance human magnetoreception through novel experimental approaches, focusing on sensory cross-talk and the possibility of affecting magnetoreception via classical conditioning and magnetosensory substitution (MSS). Despite the challenges and limitations faced, the primary contribution of this work lies in the development of a conceptual framework and the formulation of testable predictions.

The first set of proposed experiments explored whether geomagnetic information could implicitly influence established sensory processes such as the vestibulo-ocular reflex (VOR) and visual motion perception. Preliminary results were mixed but indicated a subtle influence of geomagnetic cues, particularly in visual motion perception under conditions of moderate visual coherence. The stronger geomagnetic influence observed at 60% visual coherence suggests that subliminal magnetoreception may play a supplementary role in sensory processing, especially when primary sensory information is ambiguous. However, this influence diminished in conditions of complete visual ambiguity, potentially due to a perceptual threshold. Future research should include more subjects, a wider range of visual coherence levels, and varied timing of RDK presentation in relation to magnetic rotation to clarify how implicit geomagnetic processing interacts with other sensory modalities and under what conditions it might transition to explicit perception.

The conditioning experiments, designed to associate magnetic stimuli with aversive outcomes, encountered significant challenges. The inconclusive results suggest that classical conditioning paradigms may not be ideal for studying magnetoreception in humans. The absence of a strong conditioned response and the potential blocking effect by the auditory stimulus indicate that alternative approaches should be explored. Methods such as directional training, which makes the geomagnetic information behaviorally relevant through orientation tasks, might be more effective in investigating the learnability of magnetoreception.

The sensory substitution experiments using the MESSy headband (referred to as magnetosensory substitution) provided preliminary evidence of neural plasticity associated with magnetoreceptive processing, although further testing with control conditions is necessary. EEG recordings showed changes in neural activity following training, suggesting that even brief exposure to MSS could induce neural adaptations. Regarding the behavioral results, only the visual motion perception task underwent significant changes ( $p = 0.007$ ) following MSS training. The behavioral results were less definitive, with only subtle changes observed in visual motion perception tasks. These ambiguous but non-negative findings emphasize the need for extended training periods and more ecologically valid tasks to fully assess whether these adaptations can lead to explicit, conscious use of magnetoreceptive information.

### <span id="page-43-0"></span>5.3 Overall Conclusion

This thesis explored the uncharted territory of the study of human magnetoreception. We proposed the novel hypothesis that human magnetoreception can be trained from an implicit to an explicit sense, for which we proposed and piloted experimental approaches  $(n=1)$ . To understand the role of human magnetoreception, we focused on (i) finding sensory cross-talk and (ii) forming neural associations via classical conditioning and magnetosensory substitution. Despite challenges, the work lays important groundwork for future studies.

With our preliminary findings of a subtle influence of magnetoreception on visual perception, particularly under conditions of motion ambiguity, we have begun to trace a potential pathway back to an ancient sensory ability. Magnetoreception may be integrated with the visual and vestibular systems, indicating a potential pathway for transitioning this ancient sensory ability from implicit to explicit processing. Conditioning experiments were inconclusive, indicating that traditional paradigms may not be ideal for studying magnetoreception. A one-hour training experiment using our Magnetoreception Enhancing Sensory Substitution (MESSy) headband provided initial, though ambiguous, evidence of neural plasticity; the subtle impact of this training on visual motion perception hints at the possibility of "finding our way back" to human magnetoreception, although more extensive and ecologically valid training is necessary to assess this potential fully.

In summary, while definitive enhancement of human magnetoreception from an implicit to an explicit sense was not demonstrated, this research opens promising avenues for future investigation, particularly through refined experimental designs and alternative training methods.

<span id="page-44-0"></span>Appendices

## Appendix A

# The MESSy headband

### <span id="page-46-0"></span>A.1 Tactile feedback on the head

We chose tactile feedback for the magnetosensory substitution device because it provides a 360° range of stimuli, allowing for intuitive directional information without interfering with vision or hearing. While sound-based systems can convey direction [\(Schumann and O'Regan, 2017b;](#page-59-13) [Witzel et al.,](#page-60-7) [2023\)](#page-60-7), they are impractical for our long-term goal of daily use due to interference with auditory functions .

A head-worn device was selected over waist-worn alternatives [\(Nagel et al., 2005b;](#page-58-12) [Kaspar et al.,](#page-57-11) [2014b;](#page-57-11) König et al., 2016) because head-based feedback aligns with the natural location of magnetoreceptive mechanisms, as suggested by both the quantum compass theory [\(Hore and Mourit](#page-57-15)[sen, 2016\)](#page-57-15) and the magnetite theory [\(Kirschvink,](#page-57-16) [2001;](#page-57-16) [Wiltschko and Wiltschko, 2006\)](#page-60-11). These theories propose that magnetoreceptive elements are located in the eyes or the brain (respectively), the latter supported by evidence of ferromagnetic material in the human brain [\(Kirschvink et al.,](#page-57-17) [1992a\)](#page-57-17). While this argument is less relevant in our highly controlled stationary setting, it will become relevant in future long-term experiments.

Additionally, the head is phenomenologically perceived as the center of self (specifically, right behind the eyes, see [Starmans and Bloom](#page-59-15) [\(2012\)](#page-59-15)), making head-mounted feedback more intuitive and reducing cognitive load compared to devices worn elsewhere. This alignment also supports integration with other senses, such as vision, audition, and the vestibular system. Moreover, a study has demonstrated that an implanted head-based compass can be used effectively in blind rats [\(Norimoto](#page-58-16) [and Ikegaya, 2015\)](#page-58-16).

### <span id="page-46-1"></span>A.2 Motors

Various vibration motors, including linear resonant actuators, other ERMs, and non-magnetic piezoelectric actuators, were tested during development. However, these alternatives either lacked sufficient vibrational strength for head-based feedback or produced overly audible noise. The LS-00046 ERM motors from OSEPP Electronics™were selected for their optimal balance of strong tactile feedback and minimal audibility, despite the limitation of their magnetic effects, which we accepted due to time constraints.

The MESSy headband uses these ERM motors to provide reliable and intuitive haptic feedback. The motors, rated at 3.0 V and a maximum current of 70 mA, deliver a vibration force of 1.0 G (0.098 N) within a frequency range of 160 to 330 Hz, stimulating the skin within its sensitive range with minimal power. With compact dimensions of 10 mm in diameter and 3.4 mm in length, these motors are ideal for integration into wearable devices.

### <span id="page-46-2"></span>A.3 Haptic illusion

Given that our natural senses all transduce a continuous range of stimuli, we wanted our device to emulate such continuity. With a small enough distance between two consecutive vibration motors, a person can experience an illusory singular vibration anywhere between those two motors, depending on the relative amplitude of those motors [\(Alles, 1970;](#page-56-11) [Rahal et al., 2009\)](#page-58-13). We selected thirteen motors for our design based on findings from the existing literature, which indicates that twelve equidistantly placed vibration motors around the head can produce a seamless haptic illusion of motion [\(Chu et al., 2021\)](#page-56-13). An additional motor was incorporated for practical considerations; the length of wire available necessitated the inclusion



(a) IC connected to I2C multiplexer which is here connected to only 1 haptic driver with its vibration motor. The I2C multiplexer can connect to up to 8 I2C devices.



(b) The above haptic driver plus vibration motor has been duplicated 13 times, with 6 connected to one I2C multiplexer, and 7 to the other. Also, the IMU sensor has been added to the I2C multiplexer.

Figure A.1: Schematics for the MESSy headband.

of an extra motor to encircle an average-sized head comfortably. Consequently, while not ideally precise, the motors were positioned to approximate an angular separation of 27.69 °.

#### <span id="page-48-0"></span>A.4 Compass sensor

The MESSy headband is equipped with an MPU-9250 Inertial Measurement Unit (IMU) sensor, integral to its operation in detecting and responding to directional cues. The MPU-9250, designed by InvenSense<sup>™</sup> (now part of TDK Corporation<sup>™</sup>), is a highly integrated sensor module that combines a 3-axis gyroscope, a 3-axis accelerometer, and a 3-axis magnetometer. This compact and versatile sensor is widely utilized in mobile and wearable technology due to its comprehensive sensory data capabilities and ease of integration. Currently, InvenSense ™ has been discontinued, but due to its small form factor, low power consumption, and abundance of online resources, we deemed the sensor sufficient for the prototyping phase. The sensor supports both I²C and SPI communication interfaces, allowing for flexible connection options with the Teensy™ 4.0 microcontroller used in the headband. For simplicity sake, we opted for the  $I^2C$ communication interface.

### <span id="page-48-1"></span>A.5 Sensor calibration

The MPU-9250 sensor was calibrated in the vertical position to match its mounting orientation on the headband, ensuring optimal performance in real-world use. This calibration utilized the Madgwick filter, which fuses data from the gyroscope, accelerometer, and magnetometer to estimate orientation accurately. The Madgwick filter is effective at compensating for gyroscope drift, reducing noise, and minimizing bias errors, thus providing reliable directional data.

To enhance accuracy, the calibration process accounted for the local magnetic declination in Pasadena, Los Angeles (+11.43°). This adjustment corrected the magnetometer readings for regional geomagnetic variations.

### <span id="page-48-2"></span>A.6 Sensor data processing

To minimize the impact of noise inherent in the raw sensor readings, we implemented an exponential smoothing algorithm to process the data. Exponential smoothing was chosen over alternatives such as a simple moving average due to its increased responsiveness to recent data changes. This method gives more weight to the most recent observations, thereby ensuring that the output reflects current movements more promptly, which is crucial for the real-time functionality of the device.

### <span id="page-48-3"></span>A.7 Mapping logic

The conversion of orientation data from the IMU sensor to vibrational feedback on the MESSy headband is structured through a precise mapping mechanism. Each haptic motor integrated within the headband is designated a fixed angle on a 360 degree circle. The interaction between the IMU's current orientation (yaw) and the motors' positions is governed by a linear function.

Define the angular position of each motor as  $\theta_m$ for  $m = 1, 2, \ldots, 13$ , evenly distributed around a 360-degree circle. Consequently, the angular separation between any two consecutive motors, denoted as  $\phi$ , is computed as:

$$
\phi = \frac{360^{\circ}}{13} \approx 27.6923^{\circ}.
$$

The relative angular distance between the motor's position and the IMU's current yaw orientation,  $\psi$  (between -180 and 180), is calculated using:

$$
\Delta\theta = \text{mod}\left(|\theta_m - \psi| + 180^\circ, 360^\circ\right) - 180^\circ.
$$

This measure,  $\Delta\theta$ , reflects the shortest angular difference, taking into account the circular nature of the angles.

The vibrational intensity of each motor is then determined by a linear function of  $\Delta\theta$ . Specifically, the function is designed such that:

- A  $\Delta\theta = 0^{\circ}$  (perfect alignment with the current IMU orientation) results in maximum motor vibration (100% intensity).
- A  $\Delta\theta = 2\phi$  (maximum considered angular misalignment within the functional range) results in no motor vibration (0% intensity).

The linear relationship between the vibrational intensity I and the angular difference  $\Delta\theta$  is given by the following function:

$$
I(\Delta \theta) = \max \left( 0, 1 - \frac{\Delta \theta}{2\phi} \right).
$$

This formula ensures that I) if the sensor orientation points directly to a motor, that motor vibrates at full intensity and adjacent motors (at an angular distance of  $\phi$ ) vibrate at 50% intensity. II) If the orientation is equidistant between two motors, both motors vibrate at 75% intensity, computed

as  $I(\phi/2)$ . The motors adjacent to these motors would vibrate at 25%, computed as  $I(\frac{3}{2}\phi)$ . And III), because the maximum number of active motors is four, which is the case when the orientation is exactly between two motors.

This mapping ensures that the sensory feedback is both intuitive and spatially coherent, aligning the user's directional perception with the physical feedback provided by the headband. The use of a linear scaling function simplifies the computation while adequately adapting the feedback intensity based on the orientation's deviation from the nearest motor's angle. The decision to limit the maximum number of active motors to four represents a balance between precision and the perception of continuous motion. A smaller number of active motors enhances the precision of directional feedback, particularly for the perception of North. However, it also risks making the stimulus feel more discrete rather than continuous during head rotations.

### <span id="page-49-0"></span>A.8 Fading mechanism

In the initial trials of the headband, we observed that continuous use during everyday activities could lead to sensory overload due to constant vibration. To mitigate this, we implemented a fading mechanism for the vibrations when the wearer remains stationary (i.e. when changes in their smoothed orientation do not exceed a predefined threshold). During informal evaluations conducted by the research team, this feature was found to enhance comfort significantly without diminishing the user's perception of North. Additionally, only changing magnetic fields can induce neural detection. This suggests that the fading feature of our device might align more closely with natural neural processes, making the device more intuitive, less intrusive and more likely to neurally associate with magnetoreception.

### <span id="page-49-1"></span>A.9 Shielding

One of the biggest challenges in designing a sensory substitution device for enhancing magnetoreception is that we should minimize the electromagnetic interference (see Section [2.3.2](#page-10-5) for rationale), especially since it is a head-worn device and both of the main competing magnetoreception mechanisms reside in the head. Thus, to pilot test whether we can limit the electromagnetic noise, we have tested wrapping the MESSy headband in a copper mesh fabric. As a preliminary mounting method, we first wrapped the headband in plastic wrap (to prevent shorts) and then used non-magnetic staples to attach the copper fabric around the headband. We then analyzed the RF interference using the SignalVu RF Spectrum Analyzer developed by Tektronix. The output before and after wrapping the headband are shown in Figure [A.2.](#page-50-0) Despite the observed reduction in the lower RF spectrum (0- 10 MHz), some RF radiation persists, underscoring the need for improved shielding techniques in future iterations.

<span id="page-50-0"></span>

(a) RF spectrum of the MESSy headband before



(b) RF spectrum of the MESSy headband after shielding



(c) The copper mesh fabric shielding embedded around the MESSy headband

Figure A.2: Effect of copper mesh fabric shielding on the RF spectrum of the MESSy headband. The application of a copper mesh fabric, secured with staples, significantly attenuates the major harmonics in the lower RF spectrum (0-10 MHz) emitted by the device. This attenuation is evidenced by the reduction in spectral peaks observed in Figure [A.2a](#page-50-0) compared to Figure [A.2b.](#page-50-0)

## Appendix B

# Technical Details of the Shock Circuit

<span id="page-52-0"></span>The shock circuit used in this study was originally designed in the 1990s by Mr. Victor Nenow for the Kirschvink lab at Caltech. The unit is powered by a 9V transistor radio battery, ensuring no external electrical connections are required. The shock is activated by a 0-5V TTL signal from an external computer, which connects through an optical isolation chip offering more than 5 kV isolation. A shock pulse is generated upon signal change.

The amplitude of the shock can be adjusted via a control knob, allowing participants to select a level they find comfortable. This adjustment is possible at any time during the experiment. The 0-9V signal is amplified through a small transformer to produce a 0-125V output with a maximum current of 3 mA.

During experiments, a 10 Hz square wave from the external computer activates the shock, while a separate test circuit generates a 1000 Hz signal for participant adjustment. The shock is delivered between two fingers on the same hand, ensuring no electrical signal crosses the chest or heart area, adhering to standard safety practices. This circuit was approved by the Institutional Review Board (IRB) under the chairmanship of Prof. Charlie Plott in the early 1990s.

An approximate schematic sketch of the shock circuit is illustrated in Figure [B.1.](#page-53-0)

<span id="page-53-0"></span>

Figure B.1: Circuit diagram outline sketch for the shock circuit. Tuning and voltage regulating components not shown for simplicity

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# Bibliography

- <span id="page-56-11"></span><span id="page-56-0"></span>David S. Alles. Information transmission by phantom sensations. IEEE Transactions on Man-Machine Systems, 11(1):85–91, 1970. doi: 10. 1109/TMMS.1970.299967.
- <span id="page-56-7"></span>Paul Bach-Y-Rita, Carter C. Collins, Frank A. Saunders, Benjamin White, and Lawrence Scadden. Vision Substitution by Tactile Image Projection. Nature, 221(5184):963–964, March 1969. ISSN 0028-0836, 1476-4687. doi: 10. 1038/221963a0. URL [https://www.nature.](https://www.nature.com/articles/221963a0) [com/articles/221963a0](https://www.nature.com/articles/221963a0).
- <span id="page-56-10"></span>Paul Bach-y Rita, Yuri Danilov, Mitchell Tyler, and Robert Grimm. Late human brain plasticity: vestibular substitution with a tongue BrainPort  $human-machine interface$ , volume  $40$ . Persée-Portail des revues scientifiques en SHS, 2005a.
- <span id="page-56-8"></span>Paul Bach-y Rita, Yuri Danilov, Mitchell E. Tyler, and Robert J. Grimm. Late human brain plasticity: vestibular substitution with a tongue BrainPort human-machine interface. Intellectica. Revue de l'Association pour la Recherche Cognitive, 40(1):115–122, 2005b. ISSN 0769-4113. doi: 10.3406/intel. 2005.1362. URL [https://www.persee.fr/doc/](https://www.persee.fr/doc/intel_0769-4113_2005_num_40_1_1362) [intel\\_0769-4113\\_2005\\_num\\_40\\_1\\_1362](https://www.persee.fr/doc/intel_0769-4113_2005_num_40_1_1362).
- <span id="page-56-1"></span>R Robin Baker. Human navigation and the sixth sense. Hodder and Stoughton, London, 1981. doi: 10.1086/413195.
- <span id="page-56-2"></span>RR Baker and JG Mather. A comparative approach to bird navigation: Implications of parallel studies on mammals. In Avian Navigation: International Symposium on Avian Navigation (ISAN) held at Tirrenia (Pisa), September 11–14, 1981, page 308. Springer, 1982. doi: 10.1007/978-3-642-68616-0 31.
- <span id="page-56-12"></span>Susan R. Barry. Can you acquire a sense of direction? With a compass hat, i developed a sense of direction, 2010. URL [https://www.psychologytoday.](https://www.psychologytoday.com/intl/blog/eyes-the-brain/201009/can-you-acquire-sense-direction) [com/intl/blog/eyes-the-brain/201009/](https://www.psychologytoday.com/intl/blog/eyes-the-brain/201009/can-you-acquire-sense-direction) [can-you-acquire-sense-direction](https://www.psychologytoday.com/intl/blog/eyes-the-brain/201009/can-you-acquire-sense-direction).
- <span id="page-56-6"></span>Max S. Bennett. What Behavioral Abilities Emerged at Key Milestones in Human Brain Evolution? 13 Hypotheses on the 600-Million-Year Phylogenetic History of Human Intelligence. Frontiers in Psychology, 12:685853, July 2021. ISSN 1664-1078. doi: 10.3389/fpsyg.2021. 685853. URL [https://www.frontiersin.org/](https://www.frontiersin.org/articles/10.3389/fpsyg.2021.685853/full) [articles/10.3389/fpsyg.2021.685853/full](https://www.frontiersin.org/articles/10.3389/fpsyg.2021.685853/full).
- <span id="page-56-5"></span>Christopher C Berger and H Henrik Ehrsson. Auditory motion elicits a visual motion aftereffect. Frontiers in Neuroscience, 10:559, 2016.
- <span id="page-56-13"></span>Shao-Yu Chu, Yun-Ting Cheng, Shih Chin Lin, Yung-Wen Huang, Yi Chen, and Mike Y. Chen. MotionRing: Creating Illusory Tactile Motion around the Head using 360° Vibrotactile Headbands. In The 34th Annual ACM Symposium on User Interface Software and Technology, UIST '21, pages 724–731, New York, NY, USA, October 2021. Association for Computing Machinery. ISBN 978-1-4503-8635-7. doi: 10.1145/ 3472749.3474781. URL [https://doi.org/10.](https://doi.org/10.1145/3472749.3474781) [1145/3472749.3474781](https://doi.org/10.1145/3472749.3474781).
- <span id="page-56-3"></span>Sharon A Clark, Terry Allard, William M Jenkins, and Michael M Merzenich. Receptive fields in the body-surface map in adult cortex defined by temporally correlated inputs. Nature, 332(6163): 444–445, 1988.
- <span id="page-56-9"></span>Y.P. Danilov, M.E. Tyler, K.L. Skinner, R.A. Hogle, and P. Bach-y Rita. Efficacy of electrotactile vestibular substitution in patients with peripheral and central vestibular loss. Journal of Vestibular Research, 17(2- 3):119–130, March 2008. ISSN 18786464, 09574271. doi: 10.3233/VES-2007-172-307. URL [https://www.medra.org/servlet/](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2007-172-307) [aliasResolver?alias=iospress&doi=10.](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2007-172-307) [3233/VES-2007-172-307](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2007-172-307).
- <span id="page-56-4"></span>Arnaud Delorme and Scott Makeig. Eeglab: an open source toolbox for analysis of single-trial eeg dynamics including independent component analysis. Journal of neuroscience methods, 134  $(1):9-21, 2004.$
- <span id="page-57-4"></span>Kenji Doya. Bayesian brain: Probabilistic approaches to neural coding. MIT press, 2007.
- <span id="page-57-3"></span>Svenja Engels, Nils-Lasse Schneider, Nele Lefeldt, Christine Maira Hein, Manuela Zapka, Andreas Michalik, Dana Elbers, Achim Kittel, PJ Hore, and Henrik Mouritsen. Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. Nature, 509(7500): 353–356, 2014.
- <span id="page-57-8"></span>Francisco Esteves, Cristina Parra, Ulf Dimberg, and Arne Öhman. Nonconscious associative learning: Pavlovian conditioning of skin conductance responses to masked fearrelevant facial stimuli. Psychophysiology, 31(4): 375–385, July 1994. ISSN 0048-5772, 1469- 8986. doi: 10.1111/j.1469-8986.1994.tb02446.x. URL [https://onlinelibrary.wiley.com/doi/](https://onlinelibrary.wiley.com/doi/10.1111/j.1469-8986.1994.tb02446.x) [10.1111/j.1469-8986.1994.tb02446.x](https://onlinelibrary.wiley.com/doi/10.1111/j.1469-8986.1994.tb02446.x).
- <span id="page-57-10"></span>Asif A Ghazanfar and Charles E Schroeder. Is neocortex essentially multisensory? Trends in cognitive sciences, 10(6):278–285, 2006.
- <span id="page-57-5"></span>A Gonshor. Changes of human vestibulo-ocular response induced by vision-reversal during head rotation. J Physiol, 234:102–103, 1973.
- <span id="page-57-9"></span>Alfons O Hamm, Almut I Weike, Harald T Schupp, Thomas Treig, Alexander Dressel, and Christof Kessler. Affective blindsight: intact fear conditioning to a visual cue in a cortically blind patient. Brain, 126(2):267–275, 2003.
- <span id="page-57-1"></span>Jeff Hawkins and Sandra Blakeslee. On intelligence. Macmillan, 2004.
- <span id="page-57-6"></span>Souta Hidaka, Wataru Teramoto, Yoichi Sugita, Yuko Manaka, Shuichi Sakamoto, and Yôiti Suzuki. Auditory motion information drives visual motion perception. PLoS One, 6(3):e17499, 2011.
- <span id="page-57-15"></span>Peter J Hore and Henrik Mouritsen. The radicalpair mechanism of magnetoreception. Annual review of biophysics, 45(1):299–344, 2016.
- <span id="page-57-12"></span>Kai Kaspar, Sabine König, Jessika Schwandt, and Peter König. The experience of new sensorimotor contingencies by sensory augmentation. Consciousness and Cognition, 28:47–63, 2014a. doi: 10.1016/j.concog.2014.06.006.
- <span id="page-57-11"></span>Kai Kaspar, Sabine König, Jessika Schwandt, and Peter König. The experience of new sensorimotor contingencies by sensory augmentation. Consciousness and

Cognition, 28:47–63, August 2014b. ISSN 10538100. doi: 10.1016/j.concog.2014.06.006. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S1053810014000920) [retrieve/pii/S1053810014000920](https://linkinghub.elsevier.com/retrieve/pii/S1053810014000920).

- <span id="page-57-16"></span>J Kirschvink. Magnetite-based magnetoreception. Current Opinion in Neurobiology, 11 (4):462–467, August 2001. ISSN 09594388. doi: 10.1016/S0959-4388(00)00235-X. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S095943880000235X) [retrieve/pii/S095943880000235X](https://linkinghub.elsevier.com/retrieve/pii/S095943880000235X).
- <span id="page-57-17"></span>J L Kirschvink, A Kobayashi-Kirschvink, and B J Woodford. Magnetite biomineralization in the human brain. Proceedings of the National Academy of Sciences, 89(16):7683–7687, August 1992a. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.89.16.7683. URL [https://pnas.](https://pnas.org/doi/full/10.1073/pnas.89.16.7683) [org/doi/full/10.1073/pnas.89.16.7683](https://pnas.org/doi/full/10.1073/pnas.89.16.7683).
- <span id="page-57-0"></span>Joseph L Kirschvink, Atsuko Kobayashi-Kirschvink, and Barbara J Woodford. Magnetite biomineralization in the human brain, volume 89. National Acad Sciences, 1992b. doi: 10.1073/pnas.89.16.7683.
- <span id="page-57-13"></span>Sabine U König, Frank Schumann, Johannes Keyser, Caspar Goeke, Carina Krause, Susan Wache, Aleksey Lytochkin, Manuel Ebert, Vincent Brunsch, Basil Wahn, et al. Learning new sensorimotor contingencies: Effects of longterm use of sensory augmentation on the brain and conscious perception. PloS one, 11(12): e0166647, 2016. doi: 10.1371/journal.pone. 0166647.
- <span id="page-57-7"></span>L. C. Krisst, D. Wu, B. Keyser, and S. Shimojo. The influence of geomagnetic information on visual motion. in preparation, 2024.
- <span id="page-57-14"></span>Sabine U. König, Frank Schumann, Johannes Keyser, Caspar Goeke, Carina Krause, Susan Wache, Aleksey Lytochkin, Manuel Ebert, Vincent Brunsch, Basil Wahn, Kai Kaspar, Saskia K. Nagel, Tobias Meilinger, Heinrich Bülthoff, Thomas Wolbers, Christian Büchel, and Peter König. Learning New Sensorimotor Contingencies: Effects of Long-Term Use of Sensory Augmentation on the Brain and Conscious Perception. PLOS ONE, 11(12):e0166647, December 2016. ISSN 1932-6203. doi: 10.1371/ journal.pone.0166647. URL [https://dx.plos.](https://dx.plos.org/10.1371/journal.pone.0166647) [org/10.1371/journal.pone.0166647](https://dx.plos.org/10.1371/journal.pone.0166647).
- <span id="page-57-2"></span>Stephen C Levinson. Language and cognition: The cognitive consequences of spatial description in

Guugu Yimithirr. Journal of Linguistic Anthropology, 7(1):98–131, 1997. doi: 10.1525/jlin. 1997.7.1.98.

- <span id="page-58-2"></span>Stephen C Levinson and Stephen C Levinson. Space in language and cognition: Explorations in cognitive diversity. Number 5. Cambridge University Press, 2003. doi: 10.1017/ CBO9780511613609.
- <span id="page-58-8"></span>Javier Lopez-Calderon and Steven J Luck. Erplab: an open-source toolbox for the analysis of eventrelated potentials. Frontiers in human neuroscience, 8:213, 2014.
- <span id="page-58-4"></span>Asifa Majid and Niclas Burenhult. Odors are expressible in language, as long as you speak the right language. Cognition, 130(2):266–270, 2014.
- <span id="page-58-14"></span>Lotfi B Merabet, Jascha D Swisher, Stephanie A McMains, Mark A Halko, Amir Amedi, Alvaro Pascual-Leone, and David C Somers. Combined activation and deactivation of visual cortex during tactile sensory processing. Journal of neurophysiology, 97(2):1633–1641, 2007.
- <span id="page-58-6"></span>Lotfi B Merabet, Roy Hamilton, Gottfried Schlaug, Jascha D Swisher, Elaine T Kiriakopoulos, Naomi B Pitskel, Thomas Kauffman, and Alvaro Pascual-Leone. Rapid and reversible recruitment of early visual cortex for touch.  $PLoS$  one,  $3(8)$ : e3046, 2008.
- <span id="page-58-5"></span>R Merritt, C Purcell, and G Stroink. Uniform magnetic field produced by three, four, and five square coils. Review of Scientific Instruments, 54(7):879–882, 1983.
- <span id="page-58-9"></span>Georg F Meyer and SM Wuerger. Cross-modal integration of auditory and visual motion signals. Neuroreport, 12(11):2557–2560, 2001.
- <span id="page-58-7"></span>FA Miles and JH Fuller. Adaptive plasticity in the vestibulo-ocular responses of the rhesus monkey. Brain research, 80(3):512–516, 1974.
- <span id="page-58-15"></span>Saskia K Nagel, Christine Carl, Tobias Kringe, Robert Märtin, and Peter König. Beyond sensory substitution—learning the sixth sense, volume 2. IOP Publishing, 2005a. doi: 10.1088/ 1741-2560/2/4/R02.
- <span id="page-58-12"></span>Saskia K Nagel, Christine Carl, Tobias Kringe, Robert Märtin, and Peter König. Beyond sensory substitution—learning the sixth sense. Journal of Neural Engineering, 2 (4):R13–R26, December 2005b. ISSN 1741- 2560, 1741-2552. doi: 10.1088/1741-2560/2/

4/R02. URL [https://iopscience.iop.org/](https://iopscience.iop.org/article/10.1088/1741-2560/2/4/R02) [article/10.1088/1741-2560/2/4/R02](https://iopscience.iop.org/article/10.1088/1741-2560/2/4/R02).

- <span id="page-58-0"></span>Chernetsov Nikita, Nikishena Inna, Zavarzina Natalia, and Kulbach Olga. Perception of static magnetic field by humans: a review. Biological Communications, 66(2):171–178, 2021. doi: 10.21638/spbu03.2021.208.
- <span id="page-58-16"></span>Hiroaki Norimoto and Yuji Ikegaya. Visual Cortical Prosthesis with a Geomagnetic Compass Restores Spatial Navigation in Blind Rats. Current Biology, 25(8):1091–1095, April 2015. ISSN 09609822. doi: 10.1016/j.cub.2015.02. 063. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S0960982215002651) [retrieve/pii/S0960982215002651](https://linkinghub.elsevier.com/retrieve/pii/S0960982215002651).
- <span id="page-58-11"></span>Scott D. Novich and David M. Eagleman. Using space and time to encode vibrotactile information: toward an estimate of the skin's achievable throughput. Experimental Brain Research, 233(10):2777–2788, October 2015. ISSN 0014-4819, 1432-1106. doi: 10. 1007/s00221-015-4346-1. URL [http://link.](http://link.springer.com/10.1007/s00221-015-4346-1) [springer.com/10.1007/s00221-015-4346-1](http://link.springer.com/10.1007/s00221-015-4346-1).
- <span id="page-58-10"></span>Michael V. Perrotta, Izzy Kohler, and David M. Eagleman. Bimodal Stimulation for the Reduction of Tinnitus Using Vibration on the Skin. The International Tinnitus Journal, 27(1), 2023. ISSN 09465448. doi: 10.5935/0946-5448.20230001. URL [https:](https://www.tinnitusjournal.com/articles/bimodal-stimulation-for-the-reduction-of-tinnitus-using-vibration-on-the-skin.pdf) [//www.tinnitusjournal.com/articles/](https://www.tinnitusjournal.com/articles/bimodal-stimulation-for-the-reduction-of-tinnitus-using-vibration-on-the-skin.pdf) [bimodal-stimulation-for-the-reduction-of-](https://www.tinnitusjournal.com/articles/bimodal-stimulation-for-the-reduction-of-tinnitus-using-vibration-on-the-skin.pdf)tinnitus[pdf](https://www.tinnitusjournal.com/articles/bimodal-stimulation-for-the-reduction-of-tinnitus-using-vibration-on-the-skin.pdf).
- <span id="page-58-3"></span>Peter Q Pfordresher and Steven Brown. Enhanced production and perception of musical pitch in tone language speakers. Attention, perception, & psychophysics, 71(6):1385–1398, 2009.
- <span id="page-58-1"></span>Gert Pfurtscheller and FH Lopes Da Silva. Eventrelated eeg/meg synchronization and desynchronization: basic principles. Clinical Neurophysiology, 110(11):1842–1857, 1999. doi: 10.1016/ s1388-2457(99)00141-8.
- <span id="page-58-13"></span>Lara Rahal, Jongeun Cha, and Abdulmotaleb El Saddik. Continuous tactile perception for vibrotactile displays. In 2009 IEEE International Workshop on Robotic and Sensors Environments, pages 86–91, Lecco, Italy, November 2009. IEEE. ISBN 978-1-4244-4777-0. doi: 10.1109/ROSE.2009.5355986. URL [http://](http://ieeexplore.ieee.org/document/5355986/) [ieeexplore.ieee.org/document/5355986/](http://ieeexplore.ieee.org/document/5355986/).
- <span id="page-59-6"></span>Ciro Ramos-Estebanez, Lotfi B Merabet, Katsuyuki Machii, Felipe Fregni, Gregor Thut, Timothy A Wagner, Vicenzo Romei, Amir Amedi, and Alvaro Pascual-Leone. Visual phosphene perception modulated by subthreshold crossmodal sensory stimulation. Journal of Neuroscience, 27(15):4178–4181, 2007.
- <span id="page-59-3"></span>Ralph J Roberts Jr and Christine J Aman. Developmental differences in giving directions: Spatial frames of reference and mental rotation. Child development, 64(4):1258–1270, 1993.
- <span id="page-59-5"></span>Sepideh Sadaghiani, Joost X Maier, and Uta Noppeney. Natural, metaphoric, and linguistic auditory direction signals have distinct influences on visual motion processing. Journal of Neuroscience, 29(20):6490–6499, 2009.
- <span id="page-59-14"></span>Frank Schumann and J Kevin O'Regan. Sensory augmentation: Integration of an auditory compass signal into human perception of space. Scientific Reports, 7(1):42197, 2017a. doi: 10.1038/ srep42197.
- <span id="page-59-13"></span>Frank Schumann and J. Kevin O'Regan. Sensory augmentation: integration of an auditory compass signal into human perception of space. Scientific Reports, 7(1):42197, February 2017b. ISSN 2045-2322. doi: 10.1038/ srep42197. URL [https://www.nature.com/](https://www.nature.com/articles/srep42197) [articles/srep42197](https://www.nature.com/articles/srep42197).
- <span id="page-59-1"></span>Jitendra Sharma, Alessandra Angelucci, and Mriganka Sur. Induction of visual orientation modules in auditory cortex. Nature, 404(6780):841– 847, 2000.
- <span id="page-59-7"></span>S Shimojo. Sensory modalities are not separate modalities: plasticity and interactions. Current Opinion in Neurobiology, 11(4):505–509, August 2001. ISSN 09594388. doi: 10.1016/S0959-4388(00)00241-5. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S0959438800002415) [retrieve/pii/S0959438800002415](https://linkinghub.elsevier.com/retrieve/pii/S0959438800002415).
- <span id="page-59-11"></span>Kathleen H. Sienko, Rachael D. Seidler, Wendy J. Carender, Adam D. Goodworth, Susan L. Whitney, and Robert J. Peterka. Potential Mechanisms of Sensory Augmentation Systems on Human Balance Control. Frontiers in Neurology, 9:944, November 2018. ISSN 1664-2295. doi: 10.3389/fneur.2018.00944. URL [https://www.frontiersin.org/article/](https://www.frontiersin.org/article/10.3389/fneur.2018.00944/full) [10.3389/fneur.2018.00944/full](https://www.frontiersin.org/article/10.3389/fneur.2018.00944/full).
- <span id="page-59-12"></span>K.H. Sienko, S.L. Whitney, W.J. Carender, and C. Wall. The role of sensory augmentation for people with vestibular deficits: Real-time balance aid and/or rehabilitation device? Journal of Vestibular Research, 27(1): 63–76, April 2017. ISSN 09574271, 18786464. doi: 10.3233/VES-170606. URL [https:](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-170606) [//www.medra.org/servlet/aliasResolver?](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-170606) [alias=iospress&doi=10.3233/VES-170606](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-170606).
- <span id="page-59-15"></span>Christina Starmans and Paul Bloom. Windows to the soul: Children and adults see the eyes as the location of the self. Cognition, 123(2):313–318, 2012.
- <span id="page-59-8"></span>Noelle R. B. Stiles and Shinsuke Shimojo. Auditory Sensory Substitution is Intuitive and Automatic with Texture Stimuli. Scientific Reports, 5(1):15628, October 2015. ISSN 2045- 2322. doi: 10.1038/srep15628. URL [https:](https://www.nature.com/articles/srep15628) [//www.nature.com/articles/srep15628](https://www.nature.com/articles/srep15628).
- <span id="page-59-2"></span>Yoichi Sugita. Experience in early infancy is indispensable for color perception. Current Biology, 14(14):1267–1271, 2004.
- <span id="page-59-4"></span>Kateřina Tomanová and Martin Vácha. The magnetic orientation of the antarctic amphipod gondogeneia antarctica is cancelled by very weak radiofrequency fields. Journal of Experimental Biology, 219(11):1717–1724, 2016.
- <span id="page-59-9"></span>Mitchell Tyler, Yuri Danilov, and Paul Bach-Y-Rita. CLOSING AN OPEN-LOOP CON-TROL SYSTEM: VESTIBULAR SUBSTITU-TION THROUGH THE TONGUE. Journal of Integrative Neuroscience, 02(02):159– 164, December 2003. ISSN 0219-6352, 1757- 448X. doi: 10.1142/S0219635203000263. URL [http://www.worldscientific.com/doi/](http://www.worldscientific.com/doi/abs/10.1142/S0219635203000263) [abs/10.1142/S0219635203000263](http://www.worldscientific.com/doi/abs/10.1142/S0219635203000263).
- <span id="page-59-10"></span>C. Wall and E. Kentala. Effect of displacement, velocity, and combined vibrotactile tilt feedback on postural control of vestibulopathic subjects. Journal of Vestibular Research, 20(1-2): 61–69, June 2010. ISSN 18786464, 09574271. doi: 10.3233/VES-2010-0369. URL [https:](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2010-0369) [//www.medra.org/servlet/aliasResolver?](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2010-0369) [alias=iospress&doi=10.3233/VES-2010-0369](https://www.medra.org/servlet/aliasResolver?alias=iospress&doi=10.3233/VES-2010-0369).
- <span id="page-59-0"></span>Connie X Wang, Isaac A Hilburn, Daw-An Wu, Yuki Mizuhara, Christopher P Cousté, Jacob NH Abrahams, Sam E Bernstein, Ayumu Matani, Shinsuke Shimojo, and Joseph L Kirschvink. Transduction of the geomagnetic

field as evidenced from alpha-band activity in the human brain, volume 6. Society for Neuroscience, 2019a. doi: 10.1523/ENEURO.0483-18. 2019.

- <span id="page-60-0"></span>Connie X. Wang, Isaac A. Hilburn, Daw-An Wu, Yuki Mizuhara, Christopher P. Cousté, Jacob N. H. Abrahams, Sam E. Bernstein, Ayumu Matani, Shinsuke Shimojo, and Joseph L. Kirschvink. Transduction of the Geomagnetic Field as Evidenced from alpha-Band Activity in the Human Brain. eneuro, 6(2): ENEURO.0483–18.2019, March 2019b. ISSN 2373-2822. doi: 10.1523/ENEURO.0483-18. 2019. URL [https://www.eneuro.org/lookup/](https://www.eneuro.org/lookup/doi/10.1523/ENEURO.0483-18.2019) [doi/10.1523/ENEURO.0483-18.2019](https://www.eneuro.org/lookup/doi/10.1523/ENEURO.0483-18.2019).
- <span id="page-60-4"></span>Jamie Ward and Peter Meijer. Visual experiences in the blind induced by an auditory sensory substitution device. Consciousness and Cognition, 19(1):492–500, March 2010. ISSN 10538100. doi: 10.1016/j.concog.2009.10. 006. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S1053810009001718) [retrieve/pii/S1053810009001718](https://linkinghub.elsevier.com/retrieve/pii/S1053810009001718).
- <span id="page-60-9"></span>Peter Welch. The use of fast fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. IEEE Transactions on audio and electroacoustics, 15(2):70–73, 1967.
- <span id="page-60-10"></span>Robert B Welch and David H Warren. Immediate perceptual response to intersensory discrepancy. Psychological bulletin, 88(3):638, 1980.
- <span id="page-60-6"></span>Roswitha Wiltschko and Wolfgang Wiltschko. Magnetoreception: Why Is Conditioning So Seldom Successful? Naturwissenschaften, 83(6): 241–247, June 1996. ISSN 0028-1042, 1432-1904. doi: 10.1007/s001140050281. URL [http://](http://link.springer.com/10.1007/s001140050281) [link.springer.com/10.1007/s001140050281](http://link.springer.com/10.1007/s001140050281).
- <span id="page-60-11"></span>Roswitha Wiltschko and Wolfgang Wiltschko. Magnetoreception. BioEssays, 28(2):157– 168, February 2006. ISSN 0265-9247, 1521-1878. doi: 10.1002/bies.20363. URL [https://onlinelibrary.wiley.com/doi/10.](https://onlinelibrary.wiley.com/doi/10.1002/bies.20363) [1002/bies.20363](https://onlinelibrary.wiley.com/doi/10.1002/bies.20363).
- <span id="page-60-2"></span>Roswitha Wiltschko, Peter Thalau, Dennis Gehring, Christine Nießner, Thorsten Ritz, and Wolfgang Wiltschko. Magnetoreception in birds: the effect of radio-frequency fields. Journal of the Royal Society Interface, 12(103):20141103, 2015.
- <span id="page-60-1"></span>Jonathan Winawer, Nathan Witthoft, Michael C Frank, Lisa Wu, Alex R Wade, and Lera

Boroditsky. Russian blues reveal effects of language on color discrimination. Proceedings of the national academy of sciences, 104(19):7780– 7785, 2007.

- <span id="page-60-8"></span>Christoph Witzel, Annika L¨ubbert, J Kevin O'regan, Sylvain Hanneton, and Frank Schumann. Can perception be extended to a "feel of North"? Tests of automaticity with the NaviEar. SAGE Publications Sage, London, 2021. doi: 10.1177/1059712322113023.
- <span id="page-60-7"></span>Christoph Witzel, Annika L¨ubbert, J. Kevin O'Regan, Sylvain Hanneton, and Frank Schumann. Can perception be extended to a "feel of north"? Tests of automaticity with the NaviEar. Adaptive Behavior, 31 (3):239–264, June 2023. ISSN 1059-7123, 1741-2633. doi: 10.1177/10597123221130235. URL [http://journals.sagepub.com/doi/10.](http://journals.sagepub.com/doi/10.1177/10597123221130235) [1177/10597123221130235](http://journals.sagepub.com/doi/10.1177/10597123221130235).
- <span id="page-60-5"></span>P.S. Wong, E. Bernat, S. Bunce, and H. Shevrin. Brain Indices of Nonconscious Associative Learning. Consciousness and Cognition, 6(4):519–544, December 1997. ISSN 10538100. doi: 10.1006/ccog.1997.0322. URL [https://linkinghub.elsevier.com/](https://linkinghub.elsevier.com/retrieve/pii/S1053810097903226) [retrieve/pii/S1053810097903226](https://linkinghub.elsevier.com/retrieve/pii/S1053810097903226).
- <span id="page-60-3"></span>SM Wuerger, M Hofbauer, and GF Meyer. The integration of auditory and visual motion signals at threshold. Perception  $\mathcal B$  psychophysics, 65: 1188–1196, 2003.