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The Neural Underpinnings of Allocentric Memory Encoding

Exploring the Role of Alpha and Theta
Oscillations

Bachelor's thesis in Psychology
Supervisor: Sebastian Thorp
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Preface

The current thesis was written based on an empirical research project planned and supervised by Sebastian Thorp. The author was one of eight bachelor students lucky to get admitted to the research project: “Retningssans og Brukeropplevelse i Virtuelle Virkeligheter”. The primary aim of the project was to experimentally investigate sense of direction and user experience in virtual reality, focusing on the human ability of creating allocentric representations to aid in spatial recollections. Within the concept of user experience, measures of presence, cognitive load and simulator sickness was operationalized and assessed. The implementation of electroencephalography (EEG) provided the research project with a measure of psychophysiology, which became a main component of the current thesis. The students’ contributions consisted of recruitment, administering questionnaires, lab assistance and data transfer. The author contributed recruitment and data transfer, specifically noting the coordinates resulting in the individual measures of allocentric memory accuracy. The research question and experimental hypotheses put forth in the current thesis was rooted in and drawn from existing literature relevant to the current topic. The ideas and reflections provided are of the authors own creation, as well as the choice of statistical methods. However, discussions with the supervisor provided the author with needed confirmations and valuable insights, specifically related to structure, consistency and content.

Therefore, the author extends an expression of gratitude to his supervisor, in addition to the student assistant for his work in the lab. The author would also like to thank his fellow students, providing him with a positive environment, valuable discussions, and a sense of togetherness throughout this period. Finally, the author would like to express his love and gratefulness for his family, always invested in, and supportive of his academic endeavors. The author thereby declares this work as his own.

Wordcount: approx. 9277

Abstract

Allocentric representations refer to spatial memories formed by creating cognitive maps of the environment based on salient landmarks, regardless of the individual's current or previous orientation. By recording the EEG of 30 healthy participants and employing an allocentric memory task, the current study examined whether power changes in the alpha and theta frequency bands are indicative and/or predictive of successful allocentric memory encoding in a virtual environment. Results of the present study indicate that participants who displayed high allocentric memory accuracy exhibited higher power values over anterior and posterior cortical regions within the alpha band, as well as higher power values over frontal and parietal regions within the theta band, compared to participants who displayed low allocentric memory accuracy. Furthermore, power increases within both frequency bands were found to be predictive of allocentric memory accuracy, specifically over the anterior cortical regions.

The findings of this study may contribute to the growing body of knowledge on the functionality of neural oscillations in memory processes, particularly the successful encoding of allocentric representations. Additionally, these results may have practical applications in fields such as neurology and cognitive enhancement.

The Neural Underpinnings of Allocentric Memory Encoding: Exploring the Role of Alpha and Theta Oscillations

The study of human memory has been an area of extensive research in the field of psychology, neuroscience, and cognitive science. One of the key aspects of memory is its ability to retain information about the external environment, known as spatial memory. The encoded spatial information is thought to either be represented as egocentric (i.e., location relative to the positioning of the perceiver) or allocentric “map-like” (i.e., location relative to objects and landmarks independent of the perceiver) information (Klatzky, 1998; McNamara, 2003). Allocentric memory aid humans and animals in processes such as navigation, whereby external cues are utilized to reach novel paths and destinations. This form of spatial memory is therefore thought to serve as a means to extrapolate additional information about the external environment, conjoined with, or in the absence of first-person memories (Ekstrom et al., 2014). Because of its apparent real-life and evolutionary importance, it will therefore be the focus of the current study.

As widely used in the investigation of the neural mechanisms underlying the formation and retention of memories such as spatial representations, the electroencephalogram (EEG) is regarded as a powerful tool (Ward, 2003). In particular, EEG frequency bands are thought to be indicators of different cognitive processes and have been linked to various aspects of memory performance (e.g., Axmacher et al., 2006; Başar et al., 2001; Klimesch, 1996a)

However, as apparent from a lack of available studies, an association between power changes within specific frequency bands and successful allocentric encoding has proven to be limited. This study aims to address this gap in the literature by examining the relationship between EEG frequency bands and allocentric memory encoding, employing an allocentric memory task. In order to provide a theoretical framework for the following experiment, this

study will firstly introduce the concepts of allocentric memory and EEG, and existing literature indicating how these may relate. Secondly, through a controlled laboratory experiment, the present study will investigate and test whether frequency band power in the human EEG during the encoding of object-to-object relations in virtual reality, could serve as an indication and/or predictive measure of performance in a subsequent allocentric memory task. The results of this study have the potential to build upon current research and may provide new insights into the neural mechanisms of allocentric memory formation. Additionally, these insights may have future practical applications, perhaps within the fields of neurology and cognitive enhancement (Herrmann et al., 2016).

Memory and the Human Electroencephalogram (EEG): a Theoretical Framework

Human memory is widely acknowledged to consist of multiple systems, including short-term, working, and long-term memory (LTM). Studies of amnesiac patients with spatially selective lesions have revealed distinct patterns of impairments in LTM, indicating functional and regional differences in memory (Cohen & Squire, 1980; Graf & Schacter, 1985). This led to the distinction between declarative (knowing that) and procedural (knowing how) memory, as well as the further division of declarative memory into semantic and episodic memory (Tulving, 1972). Semantic memory relates to our factual knowledge about the world, while episodic memory refers to our ability to recall information about past events (Tulving, 1983). Although not initially recognized as a separate entity in early theories of multiple memory systems, there is a specific form of LTM that is evolutionarily important and referred to as spatial memory.

Spatial Memory

Spatial memory refers to our ability to encode and retrieve information about navigational planning, and the location of objects and events in our environment. To establish position, one must use a reference point. There is agreement among some researchers that spatial memory can be processed as either egocentric or allocentric representations.

Egocentric representations relate to location relative to the individual's current or imagined position, while allocentric representations rely on memories of locations and objects in relation to other objects or landmarks in the environment, independent of the individual's current position (Klatzky, 1998; McNamara, 2003). However, this distinction has shown to be somewhat debated (Burgess, 2006; Ekstrom et al., 2014; Wang et al., 2020). For the purposes of the current study, they will nevertheless be treated as separate.

Allocentric Representation: The Cognitive Map Within the Medial Temporal Lobe (MTL)

The idea of allocentric representation can be traced back to Tolman's (1948) cognitive map theory, developed through experiments with rodents. Research has since shown that allocentric map-like representations may be facilitated and encoded by specific neurons in the MTL, such as place cells. These pyramidal neurons have been identified in the hippocampus and will selectively activate when an animal is in a particular location.

Therefore, the combined activity of numerous place cells is believed to create an allocentric representation of the environment (O'Keefe & Dostrovsky, 1971). Recent studies have argued that allocentric representations might include a broader neural network, however recognizing the hippocampus as a central structure (Ekstrom et al., 2014; Hafting et al., 2005).

The formation of new declarative memories is additionally believed to occur within this region of the MTL, specifically facilitated by the phenomenon referred to as long-term potentiation (LTP) (Bliss & Lomo, 1973). This mechanism strengthens existing synaptic

connections and promotes the formation of new ones. LTP can be induced by a single strong stimulation of the post-synaptic neuron (early phase) or by multiple stimulations in close temporal proximity (late phase). The experiments of Kandel (2001) suggest that late phase LTP is essential for the formation of allocentric representations in the rodent hippocampus. Studies suggest that optimal LTP facilitation may rely on cell-specific patterns of stimulation, alluding to the involvement of specific rhythmic activity across clusters of neurons (Bi & Poo, 2001).

Allocentric Representation as a Subset of Episodic Memory: The Memory Space

Hypothesis

Allocentric memory has been viewed as somewhat conceptually separate from the established multiple memory system theories of LTM. However, recent research has aimed to reconcile these perspectives by clarifying the way in which they interconnect. The memory space hypothesis offers a theoretical framework of hippocampal activity in relation to both spatial and declarative memory, drawing on experimental evidence that challenges the cognitive map theory (Eichenbaum & Cohen, 2014; Eichenbaum et al., 1999). Specifically, the hypothesis posits that place cell reactivity in the hippocampus reflects not only spatial information, but also temporally related changes in stimuli and behavior. This suggests that spatial representation in the hippocampus is a subset of a fundamental representation of episodic memories, which organize spatial information temporally, rather than within a map-like structure. Consequently, successful encoding of spatial information is likely to be meaningfully related to other features of episodic memories.

The Human EEG

The human EEG is a signal of electrical activity produced by the brain, and its interpretation has a wide variety of uses. For instance, in cognitive neuroscience, EEG has

shown to provide us with a recording method relating functionality of the brain to cognitive processes (Başar et al., 2001). Through the summation of inhibitory and excitatory postsynaptic potentials of cortical pyramidal neurons, the brain produces a weak electrical output signal which is recorded through electrodes and subsequently amplified by the electroencephalograph (EEG device) (Ward, 2003).

Synchronous neural activity, also known as neural oscillations, occurs when groups of neurons oscillate in a specific frequency (Hz), generating wave-like patterns that represent the temporal activation of the cells. Using mathematical techniques such as a Fourier Transform and a power spectral analysis, the EEG can be divided into specific frequency bands and the spectral power of these ranges may be determined (Muthuswamy & Thakor, 1998; Teplan, 2002; Ward, 2003). The spectral power within specific frequency bands is known to fluctuate in relation with the number of synchronously oscillating neurons, where fluctuations have been associated with diverse cognitive processes (e.g., Başar et al., 2001). Additionally, the functionality of coherent neural synchrony between local and distant cortical regions have been attributed to cortical interaction (Engel et al., 2001; Weiss & Rappelsberger, 2000).

Cognitive Correlates of the Human EEG

The traditional frequency bands ranges from 0.5 to 90Hz and are referred to as delta (0.5 – 3.5Hz), theta (4 – 7Hz), alpha (8 – 13Hz), beta (13 – 35Hz) and gamma (30 – 90Hz) (Başar, 2001; Teplan, 2002). However, the use of fixed frequency ranges has been debated, where authors such as Klimesch (1999) have argued for individual adjustments and divisions of the alpha band.

Studies have suggested that the delta band may reflect cognitive processes related to motivation, reward and inhibition (Harmony, 2013; Knyazev, 2012), while the beta band is thought to reflect sensorimotor processes (Pfurtscheller, 1981; Zaepffel et al., 2013). Theta,

alpha and gamma have been linked more closely to memory and memory-related processes such as attention, perception and information processing (e.g., Başar et al., 2001; Bosman et al., 2014; Klimesch, 1999). As the present study will analyze EEG data within the frequencies of 0.5 – 40Hz, research focusing on the functional correlates of the theta and alpha band will be described in further detail.

Alpha: Event-Related Responses Reflect Attentional Mechanisms and Memory Processes

The alpha frequency band is distinct from the other EEG bands, with its power known to either decrease or increase in response to stimuli (Klimesch, 2012). For instance, Gevins et al. (1997) reported that both low- and high-frequency alpha signals in parieto-central and occipitoparietal areas decreased with increasing task demands, supporting the "idling" hypothesis that alpha activity is mainly prominent in non-essential cortical areas (Pfurtscheller et al., 1996). Contradicting results were found in a study by Jensen et al. (2002), where alpha activity was observed to increase over parieto-occipital regions during a working memory task. The authors suggested that irrelevant cortical areas may be actively inhibited or suppressed by other areas, leading to the observed increase in alpha power.

Elaborations of this theory has since been posed in recent reviews, specifically describing topographically restricted increases as reflective of active inhibition or suppression and decreases as attentional enhancement (Foxye & Snyder, 2011; Klimesch, 2012). In support of this view, multiple studies investigating visual attention have reported decreases in alpha power over posterior cortical regions contralaterally to the attended hemifields, as well as increases over ipsilateral regions (Kelly et al., 2006; Thut et al., 2006; Yamagishi et al., 2003). Thus, modulations in the alpha band may be highly task-dependent, as attentional demands can vary widely (Foxye & Snyder, 2011; Klimesch, 2012).

Despite modulations within the alpha band seemingly being reflective of different processes of attention, its functionality in the process of memory encoding has also been

discussed. Studies have shown that good semantic memory performers exhibit a more pronounced decrease in alpha power over frontal and parieto-occipital regions, in comparison to bad performers (Hanslmayr et al., 2008; Klimesch, 1996a). Research have since also noted decreases in alpha power during the successful encoding of episodic memories (Mölle et al., 2002), in addition to the successful encoding of object placement in a spatial memory task, specifically over frontal and parietal recording sites (Sato & Yamaguchi, 2007). Although the specific role of modulations within the alpha band in memory processes seems somewhat debated, the attentional mechanisms associated with the frequency band are considered highly relevant, as attention and memory encoding are closely linked (Chun & Turk-Browne, 2007; Kuhl & Chun, 2014). Although the attentional functionality of the alpha band may result in topographical uncertainty, the weight of previous literature indicates effects to be found mainly over anterior and posterior regions.

Theta Synchronization Reflects Successful Memory Encoding

The theta frequency band is a promising candidate for reflecting successful memory encoding. As noted earlier, research suggests that optimal facilitation of LTP may depend on cell-specific activation patterns (Bi & Poo, 2001). Numerous studies have indicated that the theta rhythm may be involved in increasing LTP in the rodent hippocampus (Axmacher et al., 2006; Huerta & Lisman, 1993; Larson et al., 1986; Pavlides et al., 1988). While similar results for humans have yet to be discovered, studies employing intracranial EEG (iEEG) have revealed that hippocampal increases in theta power is indicative of successful episodic memory encoding (Lega et al., 2012), as well as virtual exploration and navigation (Caplan et al., 2003; Ekstrom et al., 2005; Watrous et al., 2011). Other researchers such as Sederberg et al. (2003) have reported results strengthening the association between intracranially recorded increases within theta and the successful encoding of memories. In this case, over the right temporal and frontal cortex.

Although the hippocampal theta rhythm has been shown to be indicative of memory encoding, measuring these signals using scalp EEG is unlikely, as pointed out by Klimesch et al. (1996b). Nevertheless, studies have demonstrated that modulations in theta power recorded at the scalp may be associated with episodic memory encoding. For example, Klimesch et al. (1996b) found increases in theta power to be predictive of subsequent recall. Recent studies have also shown similar associations between theta power and episodic memory encoding, reporting increases in theta power primarily over frontal and parietal regions (Hanslmayr et al., 2008; Mölle et al., 2002; Osipova et al., 2006; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000; White et al., 2013). Additionally, studies suggests that these regions constitute a network facilitated by coherent neural synchronization within the theta frequency band, allowing for successful memory encoding (Kawasaki et al., 2014; Sato & Yamaguchi, 2007; Sauseng et al., 2004; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000).

Promising research has also established a more direct relationship between increases in theta power recorded at the scalp, and the successful encoding of allocentric representations. For instance, a study conducted by Lithfous et al. (2015) investigating EEG frequency correlates in the encoding of cognitive maps, found that left frontal theta power increases during the encoding phase was correlated with subsequent spatial memory performance in young adults. Similar results have been reported by other researchers, associating increases in theta power over frontal and parietal regions with the successful encoding of object placement (Sato & Yamaguchi, 2007), and virtual navigation (Araújo et al., 2002).

Summary & Hypotheses

According to the reviewed literature, the strongest effects reflected in the EEG frequency bands in relation to allocentric memory are likely to be found within the alpha and

theta ranges. Specifically, increases in theta power primarily over frontal and parietal regions during encoding intervals may be indicative of higher allocentric memory accuracy (Araújo et al., 2002; Hanslmayr et al., 2008; Klimesch et al., 1996b; Lithfous et al., 2015; Mölle et al., 2002; Osipova et al., 2006; Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000; White et al., 2013).

Regarding the functionality of modulations within the alpha band, the literature indicates that successful memory encoding may be reflected as a decrease in power, primarily over anterior and posterior regions (Hanslmayr et al., 2008; Klimesch, 1996a; Mölle et al., 2002; Sato & Yamaguchi, 2007). However, considering its supposed role in attentional mechanisms, a more complex pattern may be evident. As different attentional requirements have shown to elicit different alpha responses, a unidirectional prediction of topography and specific activity is not easily determined for the current task (Gevins et al., 1997; Jensen et al., 2002; Kelly et al., 2006; Thut et al., 2006; Yamagishi et al., 2003). Given the close link between the constructs of attention and memory, modulations are nevertheless expected to be predictive of allocentric performance accuracy (Chun & Turk-Browne, 2007; Kuhl & Chun, 2014).

Based on the reviewed literature, the current study aims to test the following experimental hypotheses:

Hypothesis 1

Differences in alpha and theta power during encoding intervals will be observed between three groups based on allocentric memory accuracy.

- Hypothesis 1a: Participants with higher allocentric memory accuracy will exhibit different values of alpha power during encoding intervals, compared to participants with lower allocentric memory accuracy.

- Hypothesis 1b: Participants with higher allocentric memory accuracy will exhibit higher theta power over frontal and parietal cortical regions during encoding intervals, compared to participants with lower allocentric memory accuracy.

Hypothesis 2

Variance in alpha and theta power during encoding intervals will be predictive of allocentric memory accuracy.

- Hypothesis 2a: Variations in alpha power will be predictive of allocentric memory accuracy.
- Hypothesis 2b: Increases in theta power over frontal and parietal cortical regions during encoding intervals will be predictive of increases in allocentric memory accuracy.

Method

Participants

Sixty-two participants were recruited by the collective effort of the recruitment team for the current research project. The participants involved in this study was friends, acquaintances and fellow students of the members contributing to the research project, therefore representative of the university population at the Norwegian University of Science and Technology (NTNU). The sample consisted of subjects with normal or corrected-to-normal vision, and no history of epileptic seizures. The research project was approved by the Norwegian Centre for Research Data prior to recruitment, and each participant provided written consent before engaging in the experimental trials.

Of the 62 participants, 32 subjects were allocated to the VR condition, and therefore comprised the group which had their EEG data recorded. As data produced by subjects partaking in the VR condition was the primary focus of the present study, the remaining 30

participants were *not* included in any analyses and will therefore *not* be described in further detail. Because of missing EEG data and excessive amounts of artefacts, two subjects were removed from all analyses. The remaining sample consisted of the 17 male and 13 female subjects (20 – 26 years, $M = 22.77$, $SD = 1.431$) included in the current analyses.

Materials

Computer System

The computer used for this experiment was equipped with an Intel i7 8086K processor and Windows 10 operating system. In addition, the computer featured a Nvidia 1080 Ti graphics card and a 24-inch 1080P monitor with a 60hz refresh rate.

Head-Mounted Display (HMD)

The participants were fitted with the VR headset Meta Quest 2, which was used while they were remaining in a seated position. Meta Quest 2 features a high-resolution LCD display with 1832 x 1920 pixels per eye and a refresh rate of 90 Hz, resulting in a highly immersive visual experience. The participants were also provided with two handheld controllers, where the right-hand thumbstick was used for movement within the virtual environment. Even though the VR headset enables the user to control head movement with their own head movements, the left-hand thumbstick was configured to provide alternative head movement control. The participants were not exposed to auditive stimuli.

Procedure

Prior to Experimental Exposure

Upon their arrival at NTNU's VR-lab, the participants were instructed to take a seat in the designated waiting area. They were then provided with a consent form and a brief questionnaire, which aimed to evaluate their eligibility for the study and determine their prior

experience with video games and virtual reality (see appendix). Following the completion of these documents and the collection of their signatures, the participants were escorted into the lab, where they were given a comprehensive explanation of the task at hand. Prior to commencing the experiment, the participants were fitted with an EEG cap and conductive gel was meticulously applied under each of the 64 electrodes to reduce impedance between the scalp and the electrodes (Light et al., 2010).

Each participant was equipped with an HMD and was instructed to calibrate the settings to account for their pupillary distance. Initially, the participants were transported to a simple training environment (see figure 1), where they received instructions on how to operate the controls as described under “Materials”.

Figure 1

Training Environment



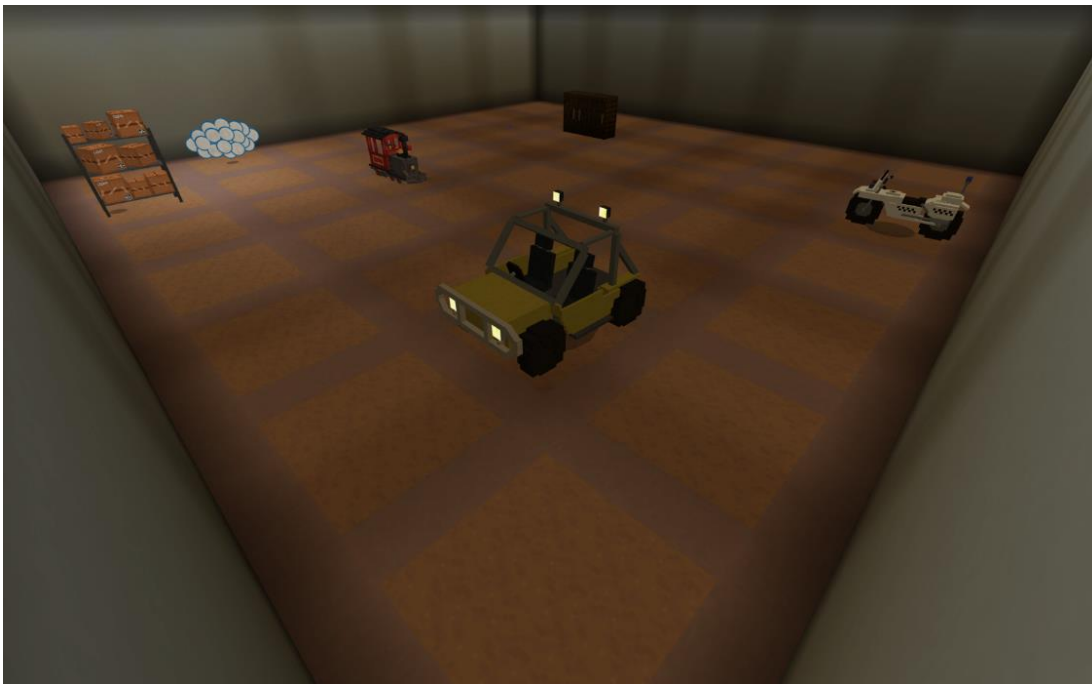
Note. Figure 1 displays the virtual training environment custom coded in Minecraft. The small rectangular area was enclosed within grey walls and comprised a small patch of grass and a single tree.

Virtual Environment

The allocentric memory encoding and virtual exploration were conducted in several custom-coded Minecraft environments. An example of the virtual environments is provided in figure 2. The virtual environments were constructed as enclosed rooms with light brown 7x7 square patterns on the floor, separated by dark-brown gridlines, and surrounded by grey walls. The objects that participants were required to remember were positioned over one of the 49 squares, and they included a dark brown closet, a shelf with cardboard boxes, a yellow car, a white motorcycle, a steam locomotive, and a cloud. The virtual exploration was enabled using command-blocks that teleported the participants to various locations. To start a new exploration sequence, a "redstone-block" was spawned at specific coordinates, which initiated the cascade of teleportation.

Figure 2

Virtual Environment



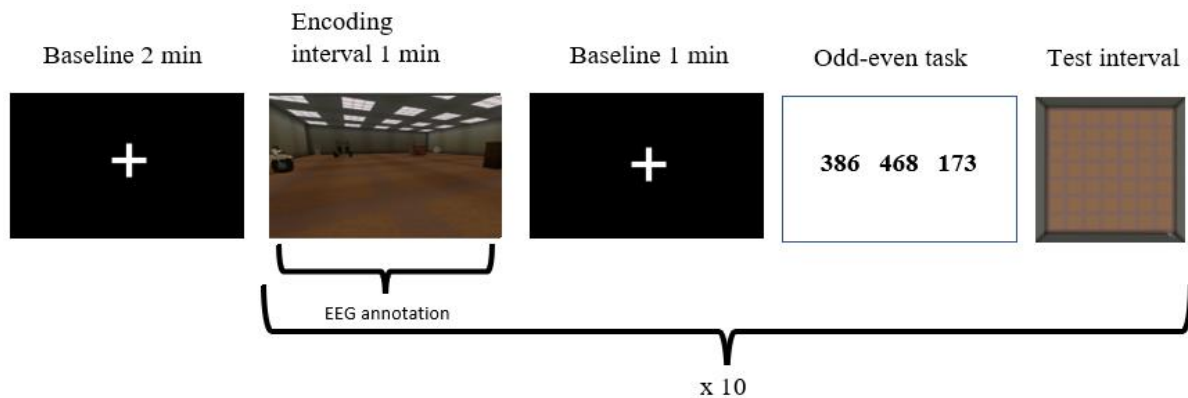
Note. Figure 2 displays the virtual environment custom coded in Minecraft. Within this enclosed room, the participants were free to explore and encode the positions of the following objects: a closet, a shelf, a car, a locomotive, a motorcycle, and a cloud.

Experimental Exposure

After the training session, the participants were directed to a baseline screen and were instructed to fixate on a white cross positioned in the center of their visual field for two minutes. The intention of the baseline screen was to obtain baseline EEG data to be used in subsequent analyses, which proved to be unnecessary. The experimental procedure involved ten encoding intervals, each followed by a test interval (see figure 3).

Figure 3

Experimental Procedure



Note. Figure 3 depicts the experimental procedure. Baseline EEG data was gathered during the first two minutes. The start and end of each encoding interval was annotated in MATLAB, and lasted for one minute. Following encoding, the participants were transported back to baseline before being subjected to an odd-even task and subsequent allocentric memory testing. The procedure from encoding to testing was repeated 10 times for each participant.

The participants were subsequently transported to the first virtual environment, where they were given one minute to freely explore and register the placement of the objects. Following the free exploration period, the participants were taken back to the baseline screen, which lasted for one minute before the HMD was removed. An odd-even task was then presented to the participants to clear their working memory, after which the test interval commenced (see figure 3).

Test Interval

During the test interval, the participants were provided with a print-out of an overhead view of the virtual environment they had explored, along with six cut-outs of the objects as displayed in figure 2. The overhead view was represented as a 7x7 grid, where objects were to be correctly placed in the corresponding boxes. A picture was taken of each finished object placement. After completing the last object placement task, the participants were asked to complete three questionnaires measuring their sense of presence (PQ; original version by Witmer et al., 2005), cognitive workload (NASA TLX; described in Hart & Staveland, 1988), and simulation sickness (SSQ; Kennedy et al., 1993) (see appendix). EEG recordings were collected throughout the experiment. However, annotations in MATLAB were used to mark the start and end of the free exploration intervals.

Measures

Calculation of Allocentric Memory Accuracy

The present study aimed to assess allocentric memory accuracy, which refers to the ability to encode and recall object locations with respect to the environment, rather than in relation to one's own body. Object placement accuracy was quantified by computing positional maps based on participants' recall of object placement in virtual environments. Specifically, each object was assigned x and y coordinates, resulting in ten distinct patterns per participant. Notably, object identity and rotation were disregarded, and only positional details were considered.

To align each pattern with a reference (i.e., the correct object placement), the Kabch-Umeyama algorithm was employed in MATLAB. The algorithm optimizes the translation, rotation, and scaling parameters of a given pattern to minimize the root-mean-square deviation (RMSD) between the transformed pattern and the reference (Kabsch, 1976, 1978;

Umeyama, 1991). Scaling was necessary to account for inter-individual differences in pattern size, which are irrelevant in measuring allocentric representation as the objects' relation to each other remains the same. Repositioning and rotation were performed because the position of objects relative to the outer boundaries of the environment was deemed irrelevant for the purposes of the current study.

Finally, each participant's allocentric memory accuracy score was computed as the average RMSD across all patterns. This score was treated as a continuous variable, where lower scores indicated greater accuracy in object placement recall. A single missing value was identified using the “missing” function in SPSS. The missing value was subsequently replaced by an imputed series mean.

EEG Recording

The EEG of 32 participants was recorded using the ANT Neuro waveguard cap with 64 Ag/AgCl electrodes and the EEGO sport amplifier (ANT Neuro, The Netherlands), and was sampled at 512Hz. The waveguard cap has built-in electrodes, adhering to the standard extended 10-20 system. CPz was used as the reference electrode, whereas AFz was used as ground electrode.

Processing of EEG Data

The raw EEG data underwent processing using the EEGLAB toolbox in MATLAB (R2023a) in order to enable spectral analysis. Prior to analysis, preprocessing was performed by implementing a script based on Makoto's preprocessing pipeline. The first step involved resampling the EEG data to 128Hz, followed by high-pass filtering at 1Hz and low-pass filtering at 40Hz using the MATLAB function "pop_eegfilternew". Additionally, identification and removal of noisy channels were performed using the "clean_rawdata()" function in EEGLAB. Subsequently, the artefact subspace reconstruction method was

employed to estimate channel signals from neighboring "clean" channels.

To extract one-minute intervals of data from the VR exposure, the annotated data was extracted from the continuous data prior to a second cleaning process. This process involved using the "pop_runica()" function to compare the present data with reference brain data and identify data that was not produced by the brain (e.g. muscle movement, eye blinks, etc.). The "IClabel" plugin was then utilized to remove data that surpassed the threshold of 80% certainty that it did not originate from the brain. To ensure data quality, data from the Oz electrode were removed for all participants, as technical issues with the EEG equipment had rendered it unusable. Furthermore, EEG data from two participants was deleted due to missing data, as well as excessive amounts of artefacts.

Data Analyses

EEG Data Analysis

Power spectral density (PSD) was calculated for each frequency of each electrode using the "spectopo()" function in EEGLAB, which yielded a power value measured in Watt/Hz. The average PSD for each frequency was calculated by using two-second hamming windows with 50% overlap.

The participants were separated into three groups based on their allocentric memory accuracy. T-tests were executed between the "high" and "low" groups on all frequencies between 1 – 49Hz on all remaining electrodes. For the purposes of the current study, the average PSD for frequencies 4-7Hz and 8-13Hz were calculated, yielding the PSD for the traditional theta and alpha frequency bands of all electrodes.

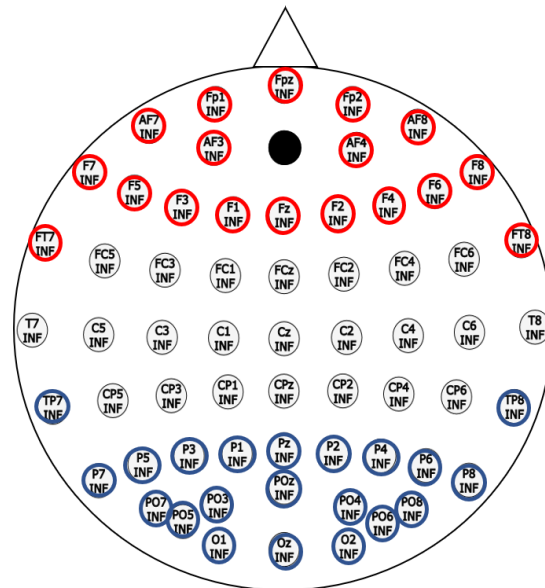
Regions of interest (ROIs)

The ROIs and resulting variables considered for the current analyses was based on findings from existing literature. The choice of specific electrodes was based on their positioning over the cortex, covering the regions deemed likely to display subsequent memory effects.

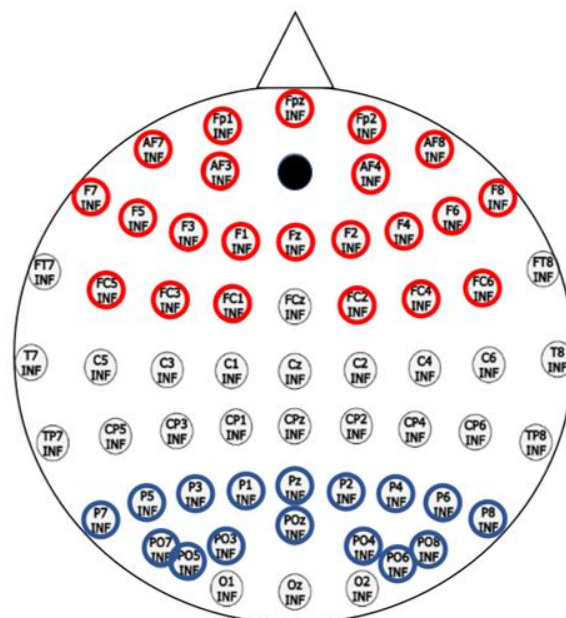
For power values within the alpha band, task-related modulations have been recorded at various areas, resulting in topographical uncertainty. Some authors have reported widespread effects over large cortical areas (Gevins et al., 1997; Jensen et al., 2002; Klimesch, 1999), others have reported topographically restricted effects specific to hemispheres, from anterior to posterior areas (Hanslmayr et al., 2008; Kelly et al., 2006; Klimesch et al., 1997; Sato & Yamaguchi, 2007; Thut et al., 2006; Yamagishi et al., 2003). As effects may reflect task-specific attentional mechanisms, exploratory analyses including all cortical lobules divided by hemispheres was assumed to be optimal.

The power values of electrodes placed over these specific areas were therefore averaged, yielding eight separate variables: left-frontal alpha (Fp1, AF3, AF7, F1, F3, F5, F7, FC1, FC3, FC5), right-frontal alpha (Fp2, AF4, AF8, F2, F4, F6, F8, FC2, FC4, FC6), left-parietal alpha (CP1, CP3, CP5, P1, P3, P5, P7), right-parietal alpha (CP2, CP4, CP6, P2, P4, P6, P8), left-occipital alpha (PO3, PO5, PO7, O1), right-occipital alpha (PO4, PO6, PO8, O2), left-temporal alpha (TP7, T7, FT7), right-temporal alpha (TP8, T8, FT8). However, subsequent analyses revealed that the intended scalp division was problematic, as described in the section “Assumption Testing”. As a result, new ROIs were computed for analyses of power values within the alpha band, dividing the cortex into two regions: anterior (Fp1, AF3, AF7, F1, F3, F5, F7, Fp2, AF4, AF8, F2, F4, F6, F8, FT7, FT8) and posterior (P1, P3, P5, P7, P2, P4, P6, P8, PO3, PO5, PO7, O1, PO4, PO6, PO8, O2, TP7, TP8 [see figure 4]).

For power values within the theta band, effects were predicted to be measured over the frontal and parietal lobules (Hanslmayr et al., 2008; Lithfous et al., 2015; Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005; White et al., 2013). Electrodes placed over the frontal and parietal lobules were pooled by averaging the obtained power values, yielding two separate variables. Frontal theta consisted of the averaged power value of electrodes: Fp1, Fp2, Fpz, AF3, AF4, AF7, AF8, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FC1, FC2, FC3, FC4, FC5, FC6. Parietal theta consisted of the averaged power value of electrodes: Pz, P1, P2, P3, P4, P5, P6, P7, P8, POz, PO3, PO4, PO5, PO6, PO7, PO8 (see figure 5).

Figure 4*ROIs for Analyses of Alpha PSD*

Note. Figure 5 displays the ROIs for the alpha frequency band used in the current analyses. PSD values of electrodes marked in similar color were averaged and yielded the PSD value of the anterior (red) and posterior (blue) regions.

Figure 5*ROIs for Analyses of Theta PSD*

Note. Figure 4 displays the ROIs for the theta frequency bands used in the current analyses. PSD values of electrodes marked in similar color were averaged and yielded the PSD value of the frontal (red) and parietal (blue) regions.

Statistics

Statistical Analyses

To examine how differences in allocentric memory accuracy relate to frequency band power, the participants were divided into three, rather than two levels of accuracy. This approach aimed to provide a more detailed and nuanced analysis of the data. Multivariate analyses of variance (MANOVA) were subsequently utilized for each frequency band. Two MANOVAs was chosen over multiple ANOVAs due to its ability to incorporate and compare differences in multiple dependent variables, resulting from the division of scalp topography within the same model. Additionally, MANOVA is recommended when the dependent variables are expected to have moderate interrelationships, and to avoid type 1 error inflation associated with multiple ANOVAs (Field, 2013, pp. 624 - 644). To account for the use of two separate analyses on the same groups, a Bonferroni correction was employed, setting the α -level at .025.

Two multiple linear regression models were fitted as to estimate the degree to which variations in allocentric performance could be predicted by modulations in both theta and alpha frequency band power during encoding intervals.

Assumption Testing

Assumptions was tested prior to any statistical analyses, as to ensure that any inferences drawn are rooted in valid results. The MANOVA analyzing differences in theta power between levels of allocentric memory accuracy contained a factor variable of three groups, and two dependent variables. The MANOVA analyzing differences in alpha power between levels of allocentric memory accuracy initially contained a factor variable of three groups, and eight dependent variables.

Considering the general discouragement of including large amounts of dependent

variables in a MANOVA with a low sample size, a need to reduce this amount became apparent for the analyses including the alpha variables (Field, 2013, p. 626). In addition, Pearson's correlation analyses were performed to assess multicollinearity between the 8 dependent variables. The analyses revealed multiple clusters of significant correlations with r values greater than .80 between adjacent recording sites in the anterior and posterior regions of the cortex. New variables for power values within the alpha band were therefore computed, reducing the number of dependent variables to two.

One multivariate outlier was identified through the application of Mahalanobis distance to the variables measuring alpha (MHD = 24.75) and theta (MHD = 27.29) power. Assessed using $p < .01$, these values were above the critical chi-square value of 9.21 for these models (Field, 2013, p. 892). Further examination revealed that extreme values for the posterior alpha and parietal theta variables were responsible for the deviation. Given the assumption that these values reflected posterior electrode issues for this participant, and that sample size equivalence among the three groups was a priority, the extreme values were replaced by imputed series means.

As this outlier may have influenced the estimates of multicollinearity, subsequent Pearson's correlations were performed. The alpha PSD variables demonstrated a strong yet reasonable correlation $r = .738$, $p < .001$. The theta PSD variables demonstrated a stronger correlation $r = .842$, $p < .001$, however within the liberal threshold of .90 (Field, 2013, p. 325).

Assessing multivariate normality is not feasible in SPSS (Field, 2013, p. 642), hence univariate normality was examined to indicate and assume multivariate normality. Interestingly, non-significant Shapiro-Wilk tests indicated within-group univariate normality for all dependent variables. However, for the group exhibiting high allocentric accuracy, the distribution of anterior alpha power showed significant leptokurtosis, $z\text{Kurtosis} = 2.13$, $p <$

.05. Additionally, the distribution of frontal theta power was significantly leptokurtic for the group exhibiting low allocentric accuracy, $zKurtosis = 2.02, p < .05$ (Field, 2013, p. 184).

Thus, the assumption of multivariate normality was deemed violated, and therefore called for the use of a robust test statistic such as Pillai's trace (Field, 2013, p. 644).

Separate scatterplot matrices for each model demonstrated linearity in the relationships between all variables within each group. The Box's test of equality of covariance matrices was not significant, indicating that the homogeneity of covariance assumption was met. To ensure the validity of follow-up analyses, Levene's tests of equality of error variances were conducted, revealing non-significant results, and affirming the absence of heteroscedasticity for all dependent variables across all groups.

Regarding the multiple linear regression models, both included two predictor variables based on the ROIs of the current study. Allocentric memory accuracy was the outcome variable for both models.

To assess the normality of the allocentric memory accuracy scores, both a Shapiro-Wilks test and an estimate of skewness and kurtosis were conducted. The Shapiro-Wilks test was not significant, and the skewness and kurtosis were within an acceptable range.

The assumptions of linearity, homoscedasticity, and normally distributed residuals were evaluated through the interpretation of a P-P plot and a scatterplot with the regression standardized residuals against the regression standardized predicted value. Based on the graphical analysis, the assumptions were satisfied for both models.

The Durbin-Watson tests were utilized to examine the assumption of independent errors, yielding values of 1.088 for model 1 and 1.084 for model 2, which fall within the acceptable range, as described by Field (2013, p. 337).

Collinearity statistics were employed to investigate multicollinearity. The variance inflation factor (VIF) found to be below 10 for all variables and the Tolerance statistic above .2 for all variables, which are deemed acceptable (Field, 2013, pp. 342 - 343).

Results

Hypothesis 1

In order to test hypothesis 1, each participant was allocated to one of three groups. The groups were determined based on the participants allocentric memory accuracy scores, where the 30 participants were divided into groups exhibiting high, decent, and low allocentric memory accuracy. Within-group descriptive statistics for hypothesis 1 are reported in table 1.

Table 1

Descriptive Statistics: Within-Group Means (Standard Deviations) N = 30

Variable	High Accuracy (n = 10)	Decent Accuracy (n = 10)	Low Accuracy (n = 10)
Anterior Alpha ^a	5.45 (5.23)	2.38 (5.66)	-3.78 (5.50)
Posterior Alpha ^a	1.57 (4.58)	1.59 (8.32)	-5.87 (6.14)
Frontal Theta ^a	8.89 (6.34)	6.97 (6.53)	-0.98 (5.60)
Parietal Theta ^a	5.02 (5.58)	5.67 (9.02)	-3.04 (6.05)
Allocentric Memory Accuracy ^b	0.67 (0.40)	2.55 (0.52)	4.51 (1.25)

Note: Groups are differentiated by allocentric memory accuracy

^a Values reflect PSD measured in Watt/Hz

^b Values reflect RSMD (i.e., lower = better)

Hypothesis 1a: Group Differences in Alpha Power

A one-way MANOVA was utilized to examine differences in alpha power over the anterior and posterior regions of the cortex, across three levels of allocentric memory accuracy. Using Pillai's Trace, the results revealed a significant overall MANOVA effect of allocentric memory accuracy on alpha power, $V = 0.41$, $F(4, 54) = 3.50$, $p = .013$, $\eta^2 = .21$. Follow up ANOVAs revealed significant main effects of allocentric memory accuracy on both anterior alpha power, $F(2, 27) = 7.36$, $p = .003$, $\eta^2 = .35$, and posterior alpha power,

$F(2, 27) = 4.34, p = .023, \eta^2 = .24$, indicating differences in alpha power over anterior and posterior regions between the three groups.

Post-hoc tests using Tukey's HSD method were conducted to examine pairwise differences among groups. The results of these analyses revealed that the participants exhibiting low allocentric memory accuracy displayed significantly lower anterior alpha power as compared to both the participants exhibiting high and decent accuracy, $M\Delta = -9.22, p = .002$ and $M\Delta = -6.14, p = .047$, respectively. However, no significant differences were found in anterior alpha power between the high and decent levels, $p = .432$.

In terms of posterior alpha power, participants exhibiting low accuracy displayed significantly lower power than the participants exhibiting decent accuracy, $M\Delta = -7.46, p = .042$, and a similar trend was observed in comparison with participants exhibiting high accuracy, $M\Delta = -7.44, p = .043$. The difference in power between participants exhibiting decent and good accuracy was not significant, $p > .999$. These findings suggest that there were differences in alpha power over the anterior and posterior regions of the cortex based on allocentric memory accuracy, and that the participants displaying low accuracy exhibited lower power in both regions compared to the other groups.

Hypothesis 1b: Group differences in theta power

A one-way MANOVA was conducted to examine differences in theta power over both frontal and parietal regions between three levels of allocentric memory accuracy. Using Pillai's trace, a significant overall MANOVA effect of allocentric memory accuracy on theta power was found, $V = .40, F(4, 54) = 3.41, p = .015, \eta^2 = .20$. Follow-up analyses consisted of two univariate ANOVAs, displaying significant differences in both frontal, $F(2, 27) = 7.19, p = .003, \eta^2 = .35$, and parietal theta power, $F(2, 27) = 4.74, p = .017, \eta^2 = .26$, between the three groups.

Tukey HSD tests was used for post hoc comparisons between the three groups. The

results revealed that participants displaying low accuracy exhibited significantly less frontal theta power as compared to the participants displaying high and decent accuracy, $Md = -9.87$, $p = .004$, $Md = -7.95$, $p = .020$, respectively. The difference between participants displaying good and decent accuracy was not significant, $p = .786$. Similar results were found for parietal theta power, where participants displaying low accuracy exhibited significantly lower parietal theta power as compared to participants displaying decent and high accuracy, $Md = -8.72$, $p = .027$, $Md = -8.06$, $p = .042$, respectively. The difference between participants displaying high and decent accuracy was not significant, $p = .977$. The findings from these analyses suggest that there were differences in theta power over the frontal and parietal regions of the cortex based on allocentric memory accuracy, and that the participants displaying low accuracy exhibited lower power in both regions compared to the other groups.

Hypothesis 2

Descriptive statistics and correlations between the variables of hypothesis 2 are reported in table 2. Results of multiple linear regression analyses are reported in tables 3 & 4.

Table 2

Descriptive Statistics and Correlations Between Study Variables (N = 30)

Variable	<i>M</i>	<i>SD</i>	1.	2.	3.	4.	5.
1. Frontal Theta ^a	4.96	7.37	-				
2. Parietal Theta ^a	2.55	7.91	.84***	-			
3. Anterior Alpha ^a	1.35	6.56	.95***	.73***	-		
4. Posterior Alpha ^a	-.90	7.24	.74***	.94***	.73***	-	
5. Allocentric Memory Accuracy ^a	2.58	1.78	-.54**	-.46*	-.59**	-.50**	-

^a Values reflect PSD measured in Watt/Hz

^b Values reflect RSMD (i.e., lower = better)

* $p < .05$ ** $p < .01$ *** $p < .001$

Table 3*Model 1: Linear Model of Predictors of Allocentric Memory Accuracy (N = 30)*

Variable	<i>b</i>	<i>SE b</i>	β	<i>t</i>	R^2	R^{2adj}
Model					.36**	.31**
Constant	2.67	0.30		9.18***		
Anterior Alpha ^a	-0.13	0.06	-0.48*	-2.07*		
Posterior Alpha ^a	-0.04	0.06	-0.15	-0.63		

* $p < .05$ ** $p < .01$ *** $p < .001$ ^a Variables measured in Watt/Hz**Table 4***Model 2: Linear Model of Predictors of Allocentric Memory Accuracy (N = 30)*

Variable	<i>b</i>	<i>SE b</i>	β	<i>t</i>	R^2	R^{2adj}
Model					.29**	.24**
Constant	3.22	0.37		8.80***		
Frontal Theta ^a	-0.13	0.07	-0.54	-1.79		
Parietal Theta ^a	-0.01	0.07	-0.01	-0.03		

* $p < .05$ ** $p < .01$ *** $p < .001$ ^a Variables measured in Watt/Hz***Hypothesis 2a: Allocentric Memory Accuracy Predicted by Alpha Power***

To examine whether power modulations within the alpha frequency band over anterior and posterior regions could predict allocentric memory accuracy, a multiple regression model was fitted and analyzed. The results revealed a significant regression equation, $F(2, 29) = 7.48$, $p = .003$, $R^{2adj} = .31$, where the model explained 31% of the variance in allocentric memory accuracy. Specifically, anterior alpha power was found to be a significant predictor of allocentric memory accuracy, where an increase of 1 Watt/Hz was associated with a .13 reduction in the participant's RSMD. However, posterior alpha power was not found to be a significant predictor of allocentric memory accuracy.

Hypothesis 2b: Allocentric Memory Accuracy Predicted by Theta Power

In order to investigate whether increases in both frontal and parietal theta power could predict allocentric memory accuracy, a multiple regression model was developed and analyzed (see table 4). The results revealed a significant regression equation, $F(2, 27) = 5.62$, $p = .009$, $R2^{adj} = .24$, where the model explained 24% of the variance in allocentric memory accuracy. However, it was found that neither frontal nor parietal theta power were significant predictors of allocentric performance accuracy.

Although the assumption of multicollinearity was deemed fulfilled, the results indicate otherwise (Mason & Perreault, 1991). As reported in previous literature, the strongest subsequent memory effects were expected to be found over frontal regions (Gevins et al., 1997; Hanslmayr et al., 2008; Lithfous et al., 2015; Mölle et al., 2002; Sauseng et al., 2004; Summerfield & Mangels, 2005; White et al., 2013). A simple linear regression only including theta power values recorded over frontal regions was fitted post-hoc, to eliminate multicollinearity and further investigate whether variations in frontal theta power could significantly predict allocentric memory accuracy.

The results revealed an overall significant regression equation, $F(1,28) = 11.66$, $p = .002$, $R^2 = .29$, where the model explained 29% of the variance in allocentric memory accuracy. Additionally, frontal theta power was found to be a significant predictor of allocentric memory accuracy, $b = -.13$, $p = .002$, where an increase of 1 Watt/Hz was associated with a reduction of RSMD equal to .13.

Discussion

Employing an allocentric memory task, the EEG of 30 healthy participants was recorded during periods of free exploration and simultaneous encoding of objects within a virtual environment. The aim of the current study was to experimentally test whether spectral data of the human EEG could indicate and/or predict the successful encoding of allocentric representations. A review of existing literature was utilized to create a theoretical framework, informing the creation of experimental hypotheses specific to the alpha and theta frequency bands.

Results of the statistical analyses revealed that participants who performed well in the allocentric memory task showed higher power values within the alpha and theta frequency bands compared to those who performed poorly. Specifically, higher alpha power was observed over both anterior and posterior recording sites, whereas higher theta power was observed over both frontal and parietal lobules. Interestingly, no significant differences in power were observed between participants displaying high and decent accuracy within both frequency bands. In addition, variations in alpha power were found to be predictive of allocentric memory accuracy, particularly over the anterior recording sites. Similarly, variations in theta power were also found to be predictive of allocentric memory accuracy, although no predictors were found to be significant in the initial model. However, fitting a simple linear regression post-hoc, it was found that increases in frontal theta power was a significant predictor of increases in allocentric memory accuracy.

Alpha Power and Allocentric Memory Accuracy

Regarding the subsequent allocentric memory effects found within the alpha band, previous studies have generally associated higher levels of memory accuracy with a decrease in power (Hanslmayr et al., 2008; Klimesch, 1996a; Mölle et al., 2002; Sato & Yamaguchi,

2007). Results of the present study produced the opposite pattern, associating increases in power with increases in allocentric memory accuracy.

However, the supposed functionality of power modulations within this frequency band has also been related to attentional mechanisms, where both decreases and increases have been associated with increasing task demands (Foxye & Snyder, 2011; Gevins et al., 1997; Jensen et al., 2002; Klimesch, 2012). As increases are thought to be reflective of active inhibition, the observations may be that of heavily attentive participants thus exhibiting higher power values over large regions of the cortex. Nevertheless, concerning this theoretical approach, cortical regions relevant for the current task would be expected to display decreases, as reported in previous research (Kelly et al., 2006; Thut et al., 2006; Yamagishi et al., 2003). Contradictory to these findings, preliminary correlation analyses revealed high correlations of power values between neighboring cortical regions. The most striking differentiation was only found between anterior and posterior regions, leading to a simple division which was used for the analyses. Although these regions displayed a somewhat different pattern of activation, higher levels of allocentric memory accuracy were associated with higher alpha power values over both regions.

One potential explanation for the observed results is that the current task required specific cortical contributions from regions not included in the analysis or not effectively captured by the EEG device. These regions may include structures located beneath the outer layers of the cortex or regions beneath electrodes exposed to excessive amounts of artefacts.

Moreover, of all the reviewed studies, Sato and Yamaguchi (2007) remains the only authors to report subsequent memory effects reflected as alpha power decrease during spatial encoding. However, it is worth noting that the task used in the current study differs significantly from the one employed by Sato and Yamaguchi (2007). In comparison, the current study provided longer and more immersive encoding intervals (60s vs. 8s), which

may have elicited divergent alpha responses. One could argue that the immersive nature of memory encoding in a VR environment may expose participants to greater amounts of stimuli, possibly resulting in increasingly rapid shifts of attention. Additionally, averaged EEG data from the ten minutes of allocentric encoding may not accurately measure event-related, topographically restrictive activation or inhibition. As a result, this measurement may reflect cognitive processes other than attention or the successful encoding object-to-object relations.

However, the current study operationalized the alpha band as the frequencies 8 – 13hz, which may have led to a wrongful interpretation of the EEG data. Klimesch (1999) have emphasized the importance of calculating the individual alpha frequency band for each participant, as the range of this frequency band varies inter-individually. This is determined based on the individual alpha frequency (IAF), which is defined as the single dominant peak frequency within the alpha band. The IAF is also correlated with the frequency that marks the transition from theta to alpha. Therefore, the individual theta band varies as a function of the individual alpha band, with frequencies below the transition frequency showing power increases in response to task demands, and frequencies above showing decreases. As reported in previous studies measuring task related changes in both frequency bands, their activity has shown to be contrasting (Hanslmayr et al., 2008; Klimesch, 1999; Mölle et al., 2002; Sato & Yamaguchi, 2007).

As such, power values of the lowest and/or highest frequencies of the current operationalization of the alpha band may have originated from frequencies outside the individual alpha band, leading to the contrasting results.

Theta Power and Allocentric Memory Accuracy

The results produced by the present study were consistent with existing literature (Araújo et al., 2002; Hanslmayr et al., 2008; Klimesch et al., 1996b; Lithfous et al., 2015; Mölle et al., 2002; Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000; White et al., 2013). Specifically, increases in theta power over both the frontal and parietal cortical regions was associated with higher allocentric memory accuracy. However, results of the initial multiple linear regression revealed that neither variations within theta power over frontal nor parietal regions were significant predictors of allocentric memory accuracy. After dropping the parietal theta variable from the model, frontal theta power was found to be a significant predictor of allocentric memory accuracy.

The lack of significant predictors in the initial regression analysis was attributed to multicollinearity, a problem where highly correlated predictors make it impossible to identify the origin of the overall effect (Mason & Perreault, 1991). These highly correlated regions may point to a fundamentally important function of the human cortical theta frequency, as long-range coherent neural synchronization have been proposed to reflect active communication and integration of information between distant cortical regions (Engel et al., 2001; Weiss & Rappelsberger, 2000). Indeed, studies suggest that coherent neural oscillations within the theta frequency band particularly within and between frontal and parietal regions may be important in the processes of memory encoding (Sato & Yamaguchi, 2007; Sauseng et al., 2004; Summerfield & Mangels, 2005). For instance, Weiss and Rappelsberger (2000) reported increased coherence within the theta frequency band between anterior and posterior recording sites during the encoding of subsequently recalled words. Furthermore, Kawasaki et al. (2014) found significant coherent synchronization in the same regions during a visual manipulation working memory task, suggesting executive processes stemming from the frontal regions interacting with and manipulating modality-specific information stemming

from the parietal regions. The results of the current study may therefore be additionally reflective of working memory processes, perhaps visual information being actively maintained and manipulated by executive functions emerging from frontal cortical regions.

However, it is important to recognize that this explanation of the current results is purely theoretical and based on simple correlations of power values between large groups of electrodes. An EEG coherence analysis of the provided data would therefore be preferred, although not available for the current study.

As the association between increases in theta power during encoding and subsequent allocentric memory accuracy was found to be significant, it would be of high interest elaborate about the theorized functionality of neurons oscillating within this frequency band. As the theta rhythm has been found to optimally induce LTP in the rodent hippocampus, one might be tempted to wonder if this effect may also be evident in humans (Axmacher et al., 2006; Huerta & Lisman, 1993; Larson et al., 1986; Pavlides et al., 1988). However, a direct observation has yet to be established. Nevertheless, using iEEG, researchers have found associations between theta oscillations emerging from the human hippocampus and successful memory encoding (Lega et al., 2012). Reports of increases in hippocampal theta power during periods of virtual navigation have also contributed to a strengthened association between increases in hippocampal theta activity and allocentric encoding (Caplan et al., 2003; Ekstrom et al., 2005; Watrous et al., 2011).

However, recording hippocampal theta oscillations at the scalp is deemed highly unlikely due to the low conductance of the EEG signal (Klimesch, 1996a). Rather, Klimesch (1996a) proposed that the association between successful memory encoding and theta measured from the scalp may be explained by the projection of hippocampal theta oscillations into the cortex through hippocampal-cortical feedback loops. The increases in theta power recorded at the scalp may therefore indirectly reflect the LTP-inducing theta

waves emerging from the hippocampus. In support of this theory, Ekstrom et al. (2005) found hippocampal theta activity to be correlated with cortical theta activity, similar to the findings reviewed by Hsieh and Ranganath (2014). However, the evidence for this theory is currently correlational, and more research is needed.

Limitations and Suggestions for Further Research

When interpreting the results, it is crucial to consider the inherent limitations of EEG research. The EEG signal represents the combined neural activity of large clusters of neurons located in the outermost layers of the cortex, which limits the specific spatial localization of cortical activity (Ward, 2003). This poses a challenge when investigating cognitive processes such as memory, which involve deeper structures such as the hippocampus, entorhinal cortex, and para hippocampal areas (Bliss & Lomo, 1973; Ekstrom et al., 2014; Kandel, 2001; O'Keefe & Dostrovsky, 1971). Further research should therefore seek to utilize EEG in conjunction with methods such as fMRI, as exemplified by White et al. (2013).

Additional limitations were also present in the current study. PSD analysis produced unexpected results, which contradict previous literature suggesting distinct event-related responses between the theta and alpha frequency bands (Hanslmayr et al., 2008; Klimesch, 1999; Mölle et al., 2002; Sato & Yamaguchi, 2007). However, upon inspection of the power values, striking similarities were observed between the two frequency bands (see Table 2). These correlations could reflect an inherent flaw of not individually adjusting the frequency bands in accordance with IAFs. As explained by Klimesch (1999), further research would benefit from individual adjustments.

However, it seems unlikely that such strong correlations would be evident with a small overlap between the frequency bands. A more probable explanation would be that the current study has collected data using faulty EEG equipment, leading to confounded results. In support of this theory, during preprocessing of the EEG data it was evident that the Oz

electrode was subjected to technical issues. Furthermore, PSD data for one participant displayed exceedingly high values over numerous posterior electrodes, as well as being uninterpretable for another. Hence, a warning is therefore presented to the reader before considering the results of the present study in future research.

Although reaching overall significance, the initial multiple regression model including the theta variables failed to indicate significant predictors. As previously mentioned, this result was attributed to multicollinearity. To address this issue, various statistical procedures were considered, such as conducting a principal component analysis on all electrodes. However, it was discovered that such a procedure would involve identifying latent variables that included power values from electrodes placed randomly over the entire scalp, rather than adhering to the ROIs of the current study. As a result, the original results were reported for transparency, and a simple linear regression was fitted post-hoc. In hindsight, a different analysis would have been preferable.

In addition to the aforementioned limitations, a few remarks on the generalizability of the current study will be considered. When interpreting the results reported in the current study, the reader should recognize that the sample consisted mainly of Norwegian students between the ages of 20 and 26 years old, which limits the generalizability of the findings to other populations. As previous research has shown, the human EEG may exhibit differences based on factors such as age and neurological conditions (Klimesch, 1999; Lithfous et al., 2015).

Moreover, the small sample size may have limited the statistical power and generalizability of the results. A larger sample size could also have reduced potential experimental fatigue, by allowing for a smaller number of experimental trials while still providing sufficient power to detect significant effects.

While the use of a contemporary HMD to allow for encoding intervals in a virtual

environment enhances the ecological validity of the study, the simplicity of the environment's design could be considered a potential limitation. Future research should aim to create more complex virtual environments that better simulate real-world situations.

Implications of the Present Study

The findings of this study may have implications for further research, as well as future practical applications. Firstly, the results indicate that spectral components of the human EEG may be a valid measure of the successful encoding of allocentric representations. However, unexpected results regarding alpha power values and the limitations of the study suggest the need for further research using various paradigms and experimental methods to strengthen this association.

Secondly, the literature investigating the relationship between EEG frequency bands and the encoding of allocentric representations has been limited. The current study may therefore contribute to the development of theories regarding the specific functionality of brain oscillations, specifically the role of theta oscillations in the formation of novel memories.

Finally, although the results of this study remain descriptive and correlational, one could imagine possible applications following future advances in technology. The current field of cognitive enhancement is rapidly progressing, and research indicates that the stimulation of cortical areas in frequencies similar to the spectral components of the human EEG elicits distinct cognitive effects (Herrmann et al., 2016). By the use of methods such as repetitive transcranial magnetic stimulation, evidence produced by the current and similar studies may have practical implications for future generations.

Conclusions

Based on the study's results, it can be concluded that changes in power within specific frequency bands of the human EEG can be used as an indicator and predictor of successful encoding of allocentric representations. The study found that participants with higher levels of allocentric memory accuracy had significantly higher power values within the alpha frequency band over anterior and posterior cortical regions, as well as within the theta frequency band over frontal and parietal regions. The study also found that increases in power values within the alpha and theta frequency bands were significantly predictive of increases in allocentric memory accuracy. Specifically, predictive effects were found over anterior cortical regions within the alpha frequency band, and over frontal regions for the theta frequency band. However, it should be noted that the study has several limitations that may have affected the results, emphasizing the need for future research.

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Appendix

Consent form

Are you interested in taking part in the research study: “*Human GPS in Virtual Environments*”?

Purpose of the project

The purpose of the present study is to investigate which brain areas are activated during a sense of direction processing task, as well as examining the impact of different levels of immersive virtual environments. Participants will be exposed to a task in virtual environments (either on a 2D screen or using VR glasses) where they will freely roam around and observe. After exposure to virtual environments individuals will be tasked by placing objects from the virtual environment on a 2D, top-down map of the environment. The results from this experiment will give insight into which brain areas are activated during tasks of spatial navigation as well as how different levels of immersive environments impact spatial navigation. The finding of this study will be helpful in better understanding how the brain processes navigational tasks and recall as well as how virtual environments impact spatial navigation. The data collected will be used, in an anonymous form, for scientific purposes, including scientific dissemination and teaching. The participant names and other personal information will not be connected with the data and not disclosed in any way.

Students that are a part of the bachelor course PSY2900, “Human GPS in Virtual Environments,” will have access to the data in an anonymized form. Students will not have access to personal data.

Who is responsible for the research project?

NTNU – Norwegian University of Science and Technology is the institution responsible for the project. This experiment is part of a research stipend granted by the Institute of Psychology at NTNU, Trondheim.

Why are you being asked to participate?

The sample of participants was selected based in the following selection criteria:

- *Generally healthy, young adults (18-30).*
- *No prior epilepsy diagnosis.*
- *Have normal-to-corrected vision.*

We need to gather some of your health data to assess whether you will be eligible to participate in this research project. If you do not entirely fulfill the above-mentioned criteria, please inform the experimenter before filling and signing the present form.

What does participation involve for you?

- If you choose to take part in this project, it involves you being fitted with EEG equipment, being exposed to virtual environments, and completing a spatial recall task. Additionally, at experiment end you will be tasked with filling three different questionnaires. You will also be asked

to fill out a short form covering general demographic information and previous experiences with virtual reality.

- The questionnaire after the exposure covers your experience with the virtual reality. All questions need to be filled out in sincere matter and should reflect your immediate response to the question. No previous knowledge is required to respond.
- For some this project will involve that you use a virtual reality headset for approximately 15 minutes. You will not have to perform any task, simply experience the simulation. Including preliminary preparations, the entire experiment will last about 60 minutes.

Participation is voluntary

Participation in the project is voluntary. If you chose to participate, you can withdraw your consent at any time without giving a reason. All information about you will then be made anonymous. There will be no negative consequences for you if you chose not to participate or later decide to withdraw.

Your personal privacy – how we will store and use your personal data

We will only use your personal data for the purpose(s) specified in this information letter. We will process your personal data confidentially and in accordance with data protection legislation (the General Data Protection Regulation and Personal Data Act).

- *We will replace your name and contact details with a code. The list of names, contact details, and respective codes will be stored separately from the rest of the collected data, Computerized data will be stored in the university computer, protected by a personal password. Data in physical format will be locked in a secured box in a locked office. The participants will be not recognizable in any way from the data.*

What will happen to your personal data at the end of the research project?

At the end of data collection (by 31.06.2023), the personal data will be anonymized. Data collected will be stored without any connection with the personal information of the participants. At the end of the study (31.12.2023), personal data will be erased.

Your rights

You have the right to:

- *access the personal data that is being processed about you.*
- *request that your personal data is deleted.*
- *request that incorrect personal data about you is corrected/rectified.*
- *receive a copy of your personal data (data portability), and*
- *send a complaint to the Data Protection Officer or The Norwegian Data Protection Authority regarding the processing of your personal data.*

[Awaiting approval: Based on an agreement with NTNU, NSD – The Norwegian Centre for Research Data has assessed that the processing of personal data in this project is in accordance with data protection legislation.]

Where can I find out more?

If you have questions about the project, or want to exercise your rights, contact:

- Researcher, Sebastian Thorp (Sebastian.Thorp@outlook.com)
- The Norwegian Centre for Research Data AS, by email: (personverntjenester@nsd.no) or by telephone: +47 55 58 21 17.
- NTNU's Data protection officer, Thomas Helgesen (Thomas.helgesen@ntnu.no)

Yours sincerely,

Researcher
Sebastian Thorp

Consent Form

I have received and understood information about the project “Human GPS in Virtual environments” and have been given the opportunity to ask questions. I give consent to the information given, and:

- To participate in collection of data using questionnaires.
- To participant in a VR environment in a lab setting
- That my data will be stored anonymously for follow up studies.

I give consent for my personal data to be processed until the end date of the project, approx. [31.12.2023]:

Sign here:

(participant, date)

Presence Questionnaire

Questionnaire sur l'État de Présence (QÉP) Laboratoire de Cyberpsychologie de l'UQO

Validation of the French-Canadian version developed by the UQO Cyberpsychology Lab:

- 101 participants completed the questionnaire following an immersion in a virtual environment;
- Cronbach's Alpha = .84
- Now 19 items (for VEs without sound/touch) et 24 items (for VEs with sounds/touch)

Scoring :

Total : Items 1 to 19 (reverse items 14, 17, 18)

- « Realism » : Items 3 + 4 + 5 + 6 + 7 + 10 + 13
- « Possibility to act » : Items 1 + 2 + 8 + 9
- « Quality of interface » : Items (all reversed) 14 + 17 + 18
- « Possibility to examine » : Items 11 + 12 + 19
- « Self-evaluation of performance » : Items 15 + 16
- « Sounds* » : Items 20 + 21 + 22
- « Haptic* » : Items 23 + 24

* NOTE : Scoring of « sounds » and « haptic » are not part of the factor analysis of the French version.

Norms (French version) :

	Moyenne	Écart type
Total	104.39	18.99
« Realism »	29.45	12.04
« Possibility to act »	20.76	6.01
« Quality of interface »	15.37	5.15
« Possibility to examine »	15.38	4.90
« Auto-évaluation de la performance »	11.00	2.87

Last version : March 2013

*Original version : Witmer, B.G. & Singer, M.J. (1998). Measuring presence in virtual environments: A presence questionnaire. *Presence : Teleoperators and Virtual Environments*, 7(3), 225-240. The factor structure of the Presence Questionnaire. *Presence*, 14(3) 298-312. Revised factor structure: Witmer, B.J., Jerome, C.J., & Singer, M.J. (2005). The factor structure of the Presence Questionnaire. *Presence*, 14(3) 298-312.

PRESENCE QUESTIONNAIRE

(Witmer & Singer, Vs. 3.0, Nov. 1994)*

Revised by the UQO Cyberpsychology Lab (2004)

Characterize your experience in the environment, by marking an "X" in the appropriate box of the 7-point scale, in accordance with the question content and descriptive labels. Please consider the entire scale when making your responses, as the intermediate levels may apply. Answer the questions independently in the order that they appear. Do not skip questions or return to a previous question to change your answer.

WITH REGARD TO THE EXPERIENCED ENVIRONMENT

1. How much were you able to control events?

NOT AT ALL	SOMEWHAT	COMPLETELY	

2. How responsive was the environment to actions that you initiated (or performed)?

NOT RESPONSIVE	MODERATELY RESPONSIVE	COMPLETELY RESPONSIVE

3. How natural did your interactions with the environment seem?

EXTREMELY ARTIFICIAL	BORDERLINE	COMPLETELY NATURAL

4. How much did the visual aspects of the environment involve you?

NOT AT ALL	SOMEWHAT	COMPLETELY	

5. How natural was the mechanism which controlled movement through the environment?

EXTREMELY ARTIFICIAL	BORDERLINE	COMPLETELY NATURAL

7. How much did your experiences in the virtual environment seem consistent with your real world experiences?

_____	_____	_____	_____	_____	_____
NOT		MODERATELY		VERY	
CONSISTENT		CONSISTENT		CONSISTENT	

8. Were you able to anticipate what would happen next in response to the actions that you performed?

_____	_____	_____	_____	_____
NOT AT ALL		SOMEWHAT		COMPLETELY

9. How completely were you able to actively survey or search the environment using vision?

_____	_____	_____	_____	_____
NOT AT ALL		SOMEWHAT		COMPLETELY

10. How compelling was your sense of moving around inside the virtual environment?

_____	_____	_____	_____	_____
NOT		MODERATELY		VERY
COMPELLING		COMPELLING		COMPELLING

11. How closely were you able to examine objects?

_____	_____	_____	_____	_____
NOT AT ALL		PRETTY		VERY
		CLOSELY		CLOSELY

12. How well could you examine objects from multiple viewpoints?

_____	_____	_____	_____	_____
NOT AT ALL		SOMEWHAT		EXTENSIVELY

13. How involved were you in the virtual environment experience?

_____	_____	_____	_____	_____	_____
NOT INVOLVED		MILDLY INVOLVED		COMPLETELY ENGROSSED	

14. How much delay did you experience between your actions and expected outcomes?

_____	_____	_____	_____	_____	_____
NO DELAYS		MODERATE DELAYS		LONG DELAYS	

15. How quickly did you adjust to the virtual environment experience?

_____	_____	_____	_____	_____	_____
NOT AT ALL		SLOWLY		LESS THAN ONE MINUTE	

16. How proficient in moving and interacting with the virtual environment did you feel at the end of the experience?

_____	_____	_____	_____	_____	_____
NOT PROFICIENT		REASONABLY PROFICIENT		VERY PROFICIENT	

17. How much did the visual display quality interfere or distract you from performing assigned tasks or required activities?

_____	_____	_____	_____	_____	_____
NOT AT ALL		INTERFERED SOMEWHAT		PREVENTED TASK PERFORMANCE	

18. How much did the control devices interfere with the performance of assigned tasks or with other activities?

_____	_____	_____	_____	_____	_____
NOT AT ALL		INTERFERED SOMEWHAT		INTERFERED GREATLY	

19. How well could you concentrate on the assigned tasks or required activities rather than on the mechanisms used to perform those tasks or activities?

_____	_____	_____	_____	_____	_____
NOT AT ALL		SOMEWHAT		COMPLETELY	

Simulation Sickness Questionnaire

No _____

Date _____

SIMULATOR SICKNESS QUESTIONNAIRE

Kennedy, Lane, Berbaum, & Lilienthal (1993)***

Instructions : Circle how much each symptom below is affecting you right now.

1. General discomfort	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
2. Fatigue	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
3. Headache	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
4. Eye strain	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
5. Difficulty focusing	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
6. Salivation increasing	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
7. Sweating	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
8. Nausea	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
9. Difficulty concentrating	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
10. « Fullness of the Head »	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
11. Blurred vision	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
12. Dizziness with eyes open	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
13. Dizziness with eyes closed	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
14. *Vertigo	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
15. **Stomach awareness	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>
16. Burping	<u>None</u>	<u>Slight</u>	<u>Moderate</u>	<u>Severe</u>

* Vertigo is experienced as loss of orientation with respect to vertical upright.

** Stomach awareness is usually used to indicate a feeling of discomfort which is just short of nausea.

Last version : March 2013

***Original version : Kennedy, R.S., Lane, N.E., Berbaum, K.S., & Lilienthal, M.G. (1993). Simulator Sickness Questionnaire: An enhanced method for quantifying simulator sickness. *International Journal of Aviation Psychology*, 3(3), 203-220.

Cognitive load questionnaire

NASA Task Load Index

Hart and Staveland's NASA Task Load Index (TLX) method assesses work load on five 7-point scales. Increments of high, medium and low estimates for each point result in 21 gradations on the scales.

Name	Task	Date

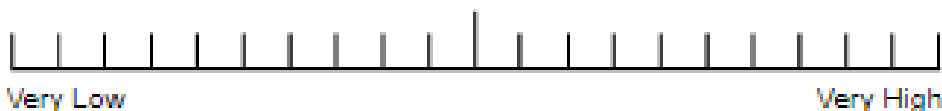
Mental Demand

How mentally demanding was the task?



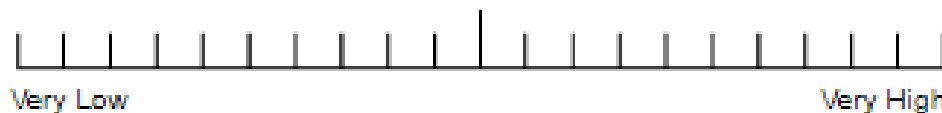
Physical Demand

How physically demanding was the task?



Temporal Demand

How hurried or rushed was the pace of the task?



Performance

How successful were you in accomplishing what you were asked to do?



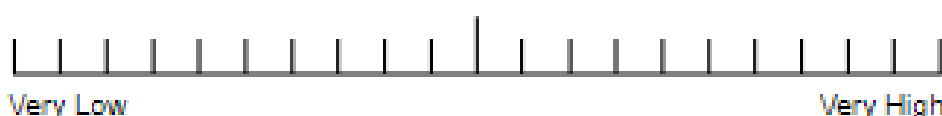
Effort

How hard did you have to work to accomplish your level of performance?



Frustration

How insecure, discouraged, irritated, stressed, and annoyed were you?



Mental Demands

How mentally fatiguing was the procedure?

**Physical Demands**

How physically fatiguing was the procedure?

**Temporal Demands**

How hurried or rushed was the pace of the procedure?

**Task Complexity**

How complex was the procedure?

**Situational Stress**

How anxious did you feel while performing the procedure?

**Distractions**

How distracting was the operating environment?



Assessment of eligibility and prior gaming experience**Assessment of eligibility and prior experience**

Age: _____

Sex (M/F): _____

Do you have normal-, or corrected to normal vision?

Y__ N__

Do you have prior epilepsy diagnosis?

Y__ N__

How frequently have you used VR in your life?

Not at all___ 0 – 1 hours___ 1 – 5 hours___ 5 hours + ___

Have you used VR in the past month?

Not at all___ 0 – 1 hours___ 1 – 3 hours___ 3 hours + ___

How many days per week do you play video games? _____

How many hours do you play video games on these days on average? _____

How many years have you been playing video games on a regular basis? _____



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