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Summary of the dissertation

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Virtual environments as a tool to study human navigation

Využití virtuálních prostředí ke studiu lidské navigace

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Abstract

Navigation is one of the most common forms of cognitive processing, which is natural for all animal species. But the neuroscientific inquiry into navigation in human subjects has been hindered by the requirements of monitoring methods, which usually require subjects to be completely still. Virtual environments allow scientists to study navigation even while the subject remains unmoving, and offer other benefits such as full control over the experimental procedures or precise behavioral recordings.

This thesis offers a basic overview of the biology of navigation and presents why navigation is an interesting cognitive process to investigate. It then presents virtual environments, explores how they can help neuroscientists to study navigation and outlines their limitations. Lastly, the literary review tries to address the question if navigation in virtual environments is comparable to navigation in the real world.

The empirical part presents five original studies of human navigation and virtual environments. These studies focus on differences of real world and virtual navigation, investigate neural pathways and brain regions involved in spatial processing, and offer examples of how virtual environments can help conduct studies otherwise impossible to do in the real world. One study provides an example of how studying navigation in a virtual environment can be interesting for psychiatry. Overall, this thesis demonstrates several benefits of VEs and the transferability of navigation results obtained in the VEs to the real world.

Keywords: virtual environments, virtual reality, navigation, spatial knowledge

Abstrakt

Navigace je jedním z nejběžnějších kognitivních procesů, který lze pozorovat u všech zvířecích druhů. Protože zobrazovací metody obvykle vyžadují, aby subjekt během experimentu zůstal bez hnutí, bylo studium navigace u lidí pomocí neurovědeckých metod dlouhou dobu obtížné. Virtuální prostředí dávají vědcům nástroj, pomocí kterého lze sledovat navigační chování u lidí i přesto, že se nehýbají. K tomu navíc přináší i další výhody, jakými je například úplná kontrola experimentálních stimulů a možnost přesného záznamu participantova chování.

Tato disertační práce podává základní přehled biologických podkladů navigace, a předkládá, proč je právě navigace zajímavým kognitivním procesem vhodným ke studiu. Dále pak prezentuje, jak mohou být virtuální prostředí pro studium navigace prospěšné a jaká jsou jejich možná úskalí. Nakonec se pokouší o zodpovězení otázky, zdali je navigace ve virtuálních prostředích srovnatelná s navigací v reálném prostoru.

Empirická část disertační práce prezentuje pět originálních vědeckých publikací, které studují virtuální prostředí a navigaci u lidí. Tyto studie se zaměřují na rozdíly mezi navigací ve virtuálním a reálném prostoru, mozkové dráhy a oblasti zapojené do prostorové kognice, a nabízí ukázky, jak virtuální prostředí umožňují uskutečnit studie, které by bez nich vzniknout nemohly. Jedna studie také poskytuje příklad toho, jak studium navigace ve virtuálních prostředích může být nápomocné v psychiatrické péči. Tato disertační práce popisuje řadu výhod virtuálních prostředí ve výzkumu navigace a přenositelnost výsledků v nich získaných pro naše porozumění navigaci v reálném světě.

Klíčová slova: virtuální prostředí, virtuální realita, navigace, prostorová orientace

Contents

1. Introduction

Navigation is one of the most common forms of cognitive processing which can be found across the entire animal domain, as all animals need to navigate to find food, shelter or mates (Grieves and Jeffery, 2017). This offers scientists a unique target of investigation which promises some degree of transferability of results between species. Navigational deficits have also been pinpointed as markers of neurological and mental disorders and pathological aging (Vlček and Laczó, 2014; Hort et al., 2007; Hanlon et al., 2006).

Virtual environments (VEs) have been a useful tool in neuroscientific research of human navigation since the early 2000s. They offer several major benefits over studying navigation in the real world:

- Economic benefit: Studies using VEs can remove both money and time constraints of real world research.
- Full control: Running experiments in the VE allows researchers to have perfect control over the presented stimuli.
- Navigating without movement: VE allows us to run navigation experiments while using imaging techniques, such as EEG, MRI, MEG, which require subjects to be completely still.
- Making the impossible possible: VE allows researchers to create situations which modify real world experiences, such as exploring non euclidean spaces or teleportation.
- Precise recordings: Experiments in VE can provide an almost perfect record of all the events that transpired, allow ex-post analyses and promote open science.

VEs also bring two major limitations, which need to be addressed in any study:

- Cognitive load, trouble with controls and gaming experience: Each participant might have different prior experience with the VEs and that can affect their performance. Increased cognitive load or unfamiliar controls can change how participants approach the task (Brunyé et al., 2017, 2018; Bartlett et al., 2020). Gaming experience have also been linked to changes in navigational strategies (West et al., 2015; Brunyé et al., 2017).
- Cybersickness: Any study with VEs and especially VR must expect that some participants might develop temporary nausea due to cybersickness. This can not only increase dropout rates and require more participants to be recruited, but can add bias to the data as cybersickness can affect different groups differently (Lawson et al., 2004; Plechatá et al., 2019; Vasser and Aru, 2020).
- Missing idiothetic cues: While navigation in the real world relies not only on external cues, such as landmarks, it can also rely on idiothetic cues - proprioceptive and vestibular input allowing navigation without sight. Some studies demonstrate that missing idiothetic cues lead to impairments in spatial learning (Holmes et al., 2018; Richardson et al., 1999; Lessels and Ruddle, 2005), although other claim that these impairments are not significant (Waller and Greenauer, 2007; Riecke et al., 2010).

Navigation in the virtual and the real world differs in important aspects, such as reduced visual fidelity, missing idiothetic cues or unnatural movement control and it is not yet clear whether the behavioral and neural responses are similar across both modalities.

2. Aims and hypotheses

The thesis aims to investigate the benefits and drawbacks of using virtual environments (VEs) to study human navigation and to offer demonstrations of such use. It also aims to assess whether navigation in VEs is representative of real world navigation and whether idiothetic cues are necessary for successful spatial learning.

Three main hypotheses were outlined:

1. Navigation in VEs leads to comparable behavior and performances as navigation in the real world

    a. People can acquire accurate spatial knowledge in VEs and apply this knowledge in the real world

    b. Navigation in the VE is comparable to navigation in the real world

2. VEs can overcome problems of real world navigation studies (such as economical feasibility) and provide more controlled experimental conditions

3. Studying navigation impairment in VEs can provide useful markers of mental disorders.

3. Overview of the studies

Study 1: How Much of What We Learn in Virtual Reality Transfers to Real-World Navigation?

Hejtmanek, L., Starrett, M., Ferrer, E., & Ekstrom, A. D. (2020). How Much of What We Learn in Virtual Reality Transfers to Real-World Navigation? *Multisensory Research*, 1–25. Impact factor: 1.829

The first study compares navigation and acquisition of spatial knowledge in the real world and in VEs. It aims to answer the question of comparability and transferability of spatial learning between the real world and VEs with or without idiothetic cues.

Methods. Participants were asked to learn the positions of offices in the real or virtual version of UC Davis Center for Neuroscience by free exploration in one of the three learning modalities (desktop VE, immersive VR with an omnidirectional treadmill or real world) and then transferred to another modality (immersive VR with an omnidirectional treadmill or real world). In each phase (learning and after transfer), participants visited 6 designated offices (out of a total of 32) 3 times and then were asked to point to them from two separate locations. Their position and behaviour in the real world were tracked using a custom iOS application, providing us with trial times and trajectories. We analysed their normalized paths, visitation errors (checking incorrect door) and pointing accuracy to assess the transfer to a new modality. We observed considerable dropout of participants (47 out of 152) due to cybersickness.

Results. While participants were learning faster in the real world than those either VE, we observed no significant differences between desktop and immersive VR. Although participants learning in the real world were acquiring the spatial knowledge the fastests, by the end of the experiment, all conditions eventually achieved almost indistinguishable performance. All these results suggest that while some aspects of navigation are still not captured by the VE, VEs lead to successful spatial learning which can be applied in the real world.

Discussion. Participants demonstrated comparable distances and visitation errors (checking incorrect doors) in all modalities upon first encountering the environment, suggesting that no modality presented unnatural complications.

Previous research suggested that formed spatial representation and neural activity are independent on learning modality (Huffman and Ekstrom, 2019). In accordance, our results demonstrate that the immersive VR allows participants to acquire the same spatial knowledge as the real world learning, but the learning process is slightly slower. However, some studies observed qualitative differences in VE learning where participants failed to achieve comparable levels of proficiency (Ruddle and Lessels, 2006). We suggest that this discrepancy might be a mere byproduct of learning rate.

Waller and Greenauer (2007) previously investigated the effect of idiothetic cues on formed spatial representation and observed that walking participants had better pointing performance in the task, although all participants' performances were quite comparable in all studied conditions. Similarly, in our experiment participants in both the immersive VR and desktop VE had comparable performance in visitation errors, distance traveled and pointing performance. However, we demonstrated that proprioceptive input was not enough to match the real world performance. It is possible that while vestibular information might be the core sensory input necessary for path integration angular accuracy (Klatzky et al., 1998; Riecke et al., 2010), the proprioceptive input can be predominantly used in distance estimations, not addressed by our design.

Unfortunate limitation of this study was the large participant dropout due to cybersickness, especially obvious in groups who spent longer time in VR. This might have created a bias in our data as more skilled navigators took less time to learn the environment, therefore spent less time in the VR and might have been less likely to succumb to cybersickness and terminate the experiment prematurely.

Participants in the real world made significantly fewer visitation errors than participants in the immersive VR. We argue that this is not an outcome of spatial learning (since the groups were comparable in their measured distances and pointing). One explanation could be that there are visual differences which can lead to failure to recognize correct doors in the VEs (all the doors in the VEs look exactly the same, but the doors in the real world can have visual tells making them easier to tell apart). However, research studying impacts of visual detail suggests that it is not important for spatial search tasks (Ruddle and Lessels, 2006). Additionally, different feedback in the VEs (automated auditory feedback) and the real world feedback (participants being told “correct” or “incorrect” by the experimenter) might have different emotional valence for the participants as receiving negative feedback from a person can have greater impact than an automated response. The mere presence of the experimenter during the real world testing could also motivate the participant to simply perform better than in the automated VE.

While we demonstrated that the spatial representation can be obtained from both the real world and virtual environments regardless of the level of immersiveness and participants might have navigated the environment in a similar manner, our results, however, do not answer any questions about the quality or neural representation of the final knowledge as the neural representation could qualitatively differ, although previous studies claim otherwise (Huffman and Ekstrom, 2019).

Conclusion. This study demonstrated differences and similarities of spatial learning in several modalities with variable idiothetic cues. Real world navigation led to fastest spatial acquisition, but by the end of the experiment participants in all modalities achieved the same spatial knowledge. Spatial knowledge acquisition was comparable when learning in desktop VE and in immersive VR with the omnidirectional treadmill, although immersive VR seemed to have provided a better platform for real world transfer.

Study 2: Mapping the scene and object processing networks by intracranial EEG

Vlcek, K. , Fajnerova, I., Nekovarova, T., **Hejtmanek, L.,** Janca, R., Jezdik, P., Kalina, A., Tomasek, M., Krsek, P., Hammer, J., Marusic, P. (2020). Mapping the scene and object processing networks by intracranial EEG. *Frontiers in Human Neuroscience*, Accepted September 2020, in press, Impact factor: 2.673

The second study uses iEEG recordings in human subjects to demonstrate that only vision is necessary to drive neural responses to spatial scenes.

Methods. We analysed iEEG data from 27 epileptic patients who viewed a set of 650 images with spatial scenes, objects, faces and fruits/vegetables. We focused on changes in broadband gamma activity (50-150Hz, BGA), bipolar referencing was used to remove the signal from distant areas. We transformed the iEEG data to the time-frequency domain using Hilbert envelope and normalized the resulting power. Using non parametric tests comparing their BGA power post and pre-stimulus, channels responding to objects and scenes were identified and mapped onto their corresponding anatomical regions of interest. We also used K-means clustering on channel MNI coordinates to find anatomically close clusters of responsive channels and matched centroids of these clusters to both documented and newly identified functional areas responsible for scene and object processing.

Results. A total 2707 bipolar channels were analyzed: 252 channels increased their BGA in response to the scene presentation and 177 out of these were responsive to both objects or scenes and 75 to scenes only. We found the scene-selective channels in the parahippocampal, lingual (and fusiform) gyrus (30% of channels), retrosplenial cortex (24% of channels), occipital cortex (11% of channels), anterior temporal cortex (11% of channels), and hippocampus (11% of channels). Using the K-means clustering we have determined seven scene-selective clusters. Some of these clusters overlapped already defined scene-selective functional areas, such as the parahippocampal place area, medial place area or occipital place area, some were localized to areas not previously observed to be scene-selective, such as the hippocampus or posterior precuneus.

Discussion. Since navigation research in VEsr relies almost exclusively on visual cues, we explored the neural signal captured by iEEG in relation to visual processing of objects and scenes.

We revealed 252 bipolar channels responding to scenes. Some of these channels were in areas previously linked to scene and landscape processing, such as parahippocampal place area (Aguirre et al., 1998), medial place area in retrosplenial-medial parietal region (O'Craven and Kanwisher, 2000) and occipital place area in the transverse occipital sulcus (Nakamura et al., 2000). We have observed scene selective channels in other areas as well, such as anterior temporal cortex and hippocampus.

To avoid any prior assumption about anatomical localization and address relative accuracy of bipolar channels' MNI coordinates, we implemented the K-means clustering algorithm, which uses the MNI coordinates and creates clusters of anatomically near channels. This approach was able to identify 7 scene-selective clusters, with one partially overlapping the occipital place area, one the parahippocampal place area and one the medial place area, all demonstrated to have spatial sensitive properties in previous studies (Aguirre et al., 1998; O'Craven and Kanwisher, 2000).

We have also found scene-selective cells in areas not previously reported. Namely, most hippocampal channels were identified to be scene selective (7 scene only, 20 in total). Hippocampus was not previously identified in humans to be scene-responding, although it has been demonstrated to contain view-dependent cells in primates (Rolls, 1999) and humans as well (Ekstrom et al., 2003), suggesting potentially larger visual modulation of hippocampal activity than observed in rats and mice.

It is necessary to ask what exactly are the implicated areas processing and if the neural signal is really coding spatial information, or if it is merely processing image complexity. Although the images were grayscaled and corrected for luminance differences, other features (such as differences in shading or edges) can also play a role during visual processing. Nevertheless, previous research indicated that spatially selective areas, such as PPA, react uniquely to scenes, rather than multitude of objects (Epstein, 2008), and we have observed similar behaviour as well.

Although almost all described functional areas related to scene processing contained channels from multiple patients, the parietal cortex had one patient supplying 4 channels and frontal cortex one channel from a single patient. This unfortunately constitutes a problem with many iEEG studies (Qasim and Jacobs, 2016). Combined with potential inaccuracies in channel localization, any general statements about functional areas have to be made cautiously.

Conclusion. Although this study was not using the VEs in establishing the neural responses, it was able to demonstrate that even static visual input is satisfactory for driving spatial-related neural responses from areas implicated in navigation.

Study 3:Spatial knowledge impairment after GPS guided navigation: Eye-tracking study in a virtual town

Hejtmánek, L., Oravcová, I., Motýl, J., Horáček, J., & Fajnerová, I. (2018). Spatial knowledge impairment after GPS guided navigation: Eye-tracking study in a virtual town. *International Journal of Human-Computer Studies*, *116*, 15–24. Impact Factor: 2.300

Study 3 investigated the impact of navigational aids on the acquisition of spatial knowledge and spatial learning. It also shows how the use of VEs can surpass some issues of navigational research, such as lack of experimental control and inaccessibility of large experimental areas in the real world.

Methods. In a large virtual town, participants followed a predetermined route from a starting position to a goal position displayed on a GPS-like map on a monitor (learning phase) and then returning back to the starting point with the map available, but without the route displayed (recall phase), completing a total of 42 there-and-back trips. In each trial, participants also pointed from goal to start and then from start to goal. Using the SR 1000 eye tracker, we tracked attention given to the GPS-like map and other parts of the screen. Participants also completed a battery of psychological tests assessing their general cognitive abilities, and a blank map tests to check how well they learned the environment.

Results. We found a significant effect of participant's attention on the GPS-like aid during learning on their navigation efficiency and pointing accuracy. Increased GPS-like aid use also led to worse blank map scores in both location placement and naming. Interestingly, participants' attention on the GPS-like aird correlated with their subjectively assessed spatial skills, so people less confident in their skills relied on it more during both learning and recall phases. We found no gender effects in navigation performance, although men had a tendency to finish the tasks faster.

Discussion. In this study, we bring a novel approach for monitoring participant's attention to the GPS-like navigational aid. Previous studies investigating the effect of navigational aids in real world environments (Ishikawa et al., 2008; Münzer et al., 2012) simply removed the aid during testing procedures, but this created an unequal situation between the conditions.

Since the modality of spatial cues during encoding can affect the quality of final representation (Münzer et al., 2012; Zhang et al., 2014), taking away the aid during testing forces participants to suddenly use a strategy they did not use during learning. Leaving the GPS-like aid present throughout the entire experiment allowed us to monitor how much the participants had used it and demonstrate that the amount of time participants looked at it was reflective of their final performance.

Previous real world navigation studies have investigated relatively smaller environments (Patai et al., 2019; Münzer et al., 2012, 2006) or traversed in cars in larger environments

(Ishikawa and Montello, 2006), which is not ideal due to different strategies and neural and behavioral correlates of route-based navigation. Using real world environments also does not allow total control over the experimental conditions, so researchers often choose to conduct the study inside a building (Richardson et al., 1999; Witmer et al., 1996), which dramatically limits the environment's size. Using VEs in this study allowed us to examine participants' behaviour in a relatively large environment with perfect control over the intervening variables.

Conclusion. Participants' spatial performance was negatively correlated with the time they spent engaged with the navigational aid. Their attention was related to participant's subjective assessment of spatial skills. VE in this case proved to be a useful tool, allowing us to investigate spatial navigation skills in a controlled, large space, while monitoring participants' attention.

Study 4: Path integration in large-scale space and with novel geometries:Comparing vector addition and encoding-error models

Harootonian, S. K., Wilson, R. C., **Hejtmánek, L.**, Ziskin, E. M., & Ekstrom, A. D. (2020). Path integration in large-scale space and with novel geometries: Comparing vector addition and encoding-error models. *PLoS Computational Biology*, *16*(5), e1007489. Impact Factor: 4.700

Study 4 investigated path integration performance in triangle completion tasks to evaluate several models potentially explaining the path integration errors and show how using VEs enables studies of navigation with or without sight in a safe environment and over long distances while preserving idiothetic cues by the use of omnidirectional treadmill.

Methods. Participants integrated path over triangles of similar sizes, but different types (isosceles, equilateral, etc.) or over a single triangle shape, but of variable scale. Participants used an omnidirectional treadmill for movement and to investigate participants' navigation without vision, controllers with haptic feedback provided them with directions.

Results. Participants underestimated homing vector (i.e. the relationship between current position and origin) distances in both experiments, and overestimated homing vector angles in Experiment 1. Angle estimations were not significantly affected by triangle type, but distance estimations were, with participants in equilateral triangles having the lowest distance error. No correlation between angle and distance errors were found. Experiment 2 showed better distance estimations for small triangles and increase of variance of distance with increasing triangle perimeter. Computational models revealed an effect of underweighting both triangle sides and effect of past trials on path integration error. Vector Addition models performed better than Error Encoding models in estimating participants' errors.

Discussion. Studying path integration on desktop VE allows precise positional recordings in infinitely large spaces, but removes idiothetic cues. These are paramount for euclidean knowledge acquisition (Chen et al., 2013), as well as decreasing path integration angular error (Waller and Greenauer, 2007; Klatzky et al., 1998; Holmes et al., 2018). VR combined with the omnidirectional treadmill allows participants to have unconstrained head movement and use proprioceptive information (such as muscle tension, number of steps and, to a limited degree, level of forward lean) and to cover infinitely large spaces in a controlled way. Overall, our results were similar to previous studies, such as homing distance underestimation and angle overestimation (Fujita et al., 1993; Loomis et al., 1993).

There was also no correlation between angular and distance errors. Firstly, this could be caused by the independence of two sensory inputs. While the rotational components were unhindered and participants had complete freedom of head and body movement, they could not really move forward, only lean forward and walk in place. The importance for rotational idiothetic input has been demonstrated to be more important for successful path integration than translation cues (Riecke et al., 2010; Waller et al., 1998), although other researchers argue that both inputs are necessary for spatial updating (Chance et al., 1998).

Previous path integration studies done in real environments used triangles in much smaller sizes (Loomis et al., 1993; Klatzky et al., 1998). Path integration over short distances can be relatively easy, and it is not clear how effective it can be over distances as large as half a kilometer. To prevent any dangers and intervening cues, path integration studies have also been conducted in locations of limited size, e.g. indoor sports fields (Stangl et al., 2020) or hallways (Waller and Greenauer, 2007). Using the VR setup with the omnidirectional treadmill, the experiment 2 was able to explore large spaces of hundreds of meters long and demonstrate that size of the triangle does not necessarily affect the homing vector's angular error, while it does increase the distance errors logarithmically.

Usual path integration tasks in real world put participants in a stressful environment, usually being blindfolded and guided by the experimenter actively leading them or pulling them behind the experimenter (Stangl et al., 2020; Loomis et al., 1993). They might also be afraid of hitting a potential obstacle or a wall when walking to the original destination and choose a more cautious strategy. By using a VE with the treadmill, it is possible to remove these limitations, while keeping the proprioceptive and vestibular input relatively intact.

Conclusion. Using VEs in this case allowed us to investigate path integration over infinitely large spaces not previously studied in path navigation with proprioceptive inputs and have precise recordings of participants trajectories. We were also able to investigate triangle completion tasks with visual beaconing, which would be practically impossible to do over longer distances in the real world.

Study 5: Virtual Supermarket Shopping Task for cognitive assessment and rehabilitation of psychiatric patients: Validation in chronic schizophrenia.

Plechatá, A., **Hejtmánek, L.,** Fajnerová, I. Virtual Supermarket Shopping Task for cognitive assessment and rehabilitation of psychiatric patients: Validation in chronic schizophrenia. *Československá psychologie*, accepted September 2020, in press. Impact Factor: 0.373

Study 5 uses VE to investigate the memory and navigation impairment accompanying mental disorders and documents this impairment in a group of schizophrenia patients.

Methods. A Virtual Supermarket Shopping Task (VSST) was designed to address patients' short term memory, spatial memory as well as planning and execution skills. Twenty patients and twenty healthy controls were asked to familiarize themselves with the supermarket VE, then asked to remember lists of items (at difficulty of 3, 5, 7 or 9 shopping items) and collect them as fast as possible and in the shortest distance. They were also tested with a battery of neuropsychological tests Rey Auditory Verbal Learning Test, Logical Memory, Trail Making Test, PEBL Continuous performance task, Positive and Negative Syndrome Scale, Beck's depression and anxiety inventory and Global Assessment of Functioning. We assessed VSST convergent and divergent validity with the existing neuropsychological measures. We also explored the relationship of VSST performance to participant's condition and demographics.

Results. VSST performance was severely impaired in SZ patients in higher difficulties (7 or 9 items) but not in lower difficulties. We observed that SZ patients tend to take longer time per distance travelled, suggesting longer planning or orientation pauses. VSST task performance correlated with neuropsychological scales, suggesting the task targets similar executive and memory processes as the current methods. We found some effects of gender on performance and age on trial distance and time, but no effect of gaming experience in VSST performance. We suggest that VSST can offer few benefits such as increased ecological validity, automated administration, possibility of remote administration, and addressing navigation performance not commonly present in neuropsychological assessment.

Discussion. Schizophrenia (SZ) patients performed significantly worse in VSST than healthy controls in all trials except the easiest. The observed performance in VSST correlated with existing metrics of memory, suggesting that the task addresses similar deficits as standardized tests. Surprisingly, we have not been able to link it directly to SZ symptomatology. Patients' navigation results were not significantly correlated with PANSS scores, which is contradictory to findings from other studies linking negative symptomatology to worse cognitive performance in standardized tests (Bezdicek et al., 2020) and spatial tasks (Folley et al., 2010).

VSST also allows precise recordings of participants' behaviours and tracking metrics not addressed by standard neuropsychological batteries. These include route planning, or spatial deficits. In this study, we focused primarily on trial distances. Although the distance measure is a very simple metric non respective of varying strategies, goal directed behavior, repetitive route following or other heuristics potentially indicative of the disorder, it could mark navigational deficits.

Interestingly, SZ patients need longer times to travel the same distance. This behavior can be explained in several ways. Either the demonstrated worse performance was due to slower processing speed and executive functions, reported to be impaired in SZ (Fioravanti et al., 2012) and the spatial skills themselves were unaffected, or SZ patients could give up on the task earlier.

We also observed the impact of age on navigation times (increasing with age) and marginal impact on distances (decreasing with age). VE can unnecessarily and unevenly increase cognitive load to different populations which could lead to older participants might simply performing worse in certain VE tasks due to the unfamiliarity with the controls or the task.

Conclusion. Similar tasks could not be conducted in real environments because of their cost and time requirements. Use of VE allowed us to precisely record participants' behaviours and control for extraneous variables, while simulating a sufficient representation of activity of daily living with clear behavioral correlates to patients' condition. Closer investigation of mnemonic and navigational strategies and identifying individual differences could lead to a promising diagnostic application.

4. Conclusions

Addressing the aims and hypotheses, study 1 demonstrated the comparability of VE vs real world navigation and offered some insights into potential complications of VE use and limitations of VE to real world spatial knowledge transfer, such as cybersickness. It used the possibility of obtaining precise recordings of participant's movements and comparing them directly between the real world and the VE.

The second study did not use VE directly, but used iEEG recordings in human subjects to demonstrate that only vision is necessary to drive neural responses to spatial scenes and addressing the comparability of visually-only driven spatial cognition.

Study 3 and study 4 demonstrate the usefulness of VE and show how VE can solve the problems of economical feasibility and machinery requiring stillness and provide full control over experimental conditions. It also benefited from precise recordings, as we were able to document participants' exact movements in path integration paths of several hundred meters long, not previously recorded in human subjects.

The last presented study used VE to investigate memory and navigation impairment accompanying mental disorders and documented this impairment in a group of schizophrenia patients.

To conclude, VEs are an incredibly useful tool in neuroscientific research of navigation. They allow navigators to remain stable while moving through the world and therefore providing researchers an opportunity to collect neural and physiological recordings. Thanks to the VEs, researchers can precisely record the entire experimental procedures and freely modify and control the environments, which would be economically impossible or quite challenging to do in the real world.

While the VEs and the associated hardware are still not perfect, navigation in a VE can cause nausea and introduce confounding factors to collected data, these systems are rapidly improving. New generations of head mounted devices offer better head and body tracking and new levels of interactivity, and dramatically enhance the felt presence and have the potential to reduce cybersickness, and improvements in graphical hardware and software can provide almost photorealistic rendering of environments. Overall, VEs seem to be indispensable for navigation research, enabling experiments that would be not possible without them.

Bibliography

Aguirre, G. K., Zarahn, E., and D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: evidence and implications. *Neuron*, 21(2):373–383.

Bartlett, M. L., Scott Gwinn, O., Thomas, N. A., and Nicholls, M. E. R. (2020). Cognitive load exacerbates rightward biases during computer maze navigation. *Brain Cogn.*, 140:105547.

Bezdicek, O., Michalec, J., Kališová, L., Kufa, T., Děchtěrenko, F., Chlebovcová, M., Havlík, F., Green, M. F., and Nuechterlein, K. H. (2020). Profile of cognitive deficits in schizophrenia and factor structure of the czech MATRICS consensus cognitive battery. *Schizophr. Res.*, 218:85–92.

Brunyé, T. T., Martis, S. B., and Taylor, H. A. (2018). Cognitive load during route selection increases reliance on spatial heuristics. *Q. J. Exp. Psychol.*, 71(5):1045–1056.

Brunyé, T. T., Wood, M. D., Houck, L. A., and Taylor, H. A. (2017). The path more travelled: Time pressure increases reliance on familiar route-based strategies during navigation. *Q. J. Exp. Psychol.*, 70(8):1439–1452.

Chance, S. S., Gaunet, F., Beall, A. C., and Loomis, J. M. (1998). Locomotion mode affects the updating of objects encountered during travel: The contribution of vestibular and proprioceptive inputs to path integration. *Presence: Teleoperators and Virtual Environments*, 7(2):168–178.

Chen, G., King, J. A., Burgess, N., and O'Keefe, J. (2013). How vision and movement combine in the hippocampal place code. *Proc. Natl. Acad. Sci. U. S. A.*, 110(1):378–383.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., and Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, 425(6954):184–188.

Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation.

Fioravanti, M., Bianchi, V., and Cinti, M. E. (2012). Cognitive deficits in schizophrenia: an updated metanalysis of the scientific evidence. *BMC Psychiatry*, 12:64.

Folley, B. S., Astur, R., Jagannathan, K., Calhoun, V. D., and Pearlson, G. D. (2010). Anomalous neural circuit function in schizophrenia during a virtual morris water task. *Neuroimage*, 49(4):3373–3384.

Fujita, N., Klatzky, R. L., Loomis, J. M., and Golledge, R. G. (1993). The encoding-error model of pathway completion without vision. *Geogr. Anal.*, 25(4):295–314.

Grieves, R. M. and Jeffery, K. J. (2017). The representation of space in the brain. *Behav. Processes*, 135:113–131.

Hanlon, F. M., Weisend, M. P., Hamilton, D. A., Jones, A. P., Thoma, R. J., Huang, M., Martin, K., Yeo, R. A., Miller, G. A., and Cañive, J. M. (2006). Impairment on the hippocampal-dependent virtual morris water task in schizophrenia. *Schizophr. Res.*, 87(1-3):67–80.

Holmes, C. A., Newcombe, N. S., and Shipley, T. F. (2018). Move to learn: Integrating spatial information from multiple viewpoints. *Cognition*, 178:7–25.

Hort, J., Laczo, J., Vyhnalek, M., Bojar, M., Bures, J., and Vlcek, K. (2007). Spatial navigation deficit in amnestic mild cognitive impairment. *Proceedings of the National Academy of Sciences*, 104(10):4042–4047.

Huffman, D. J. and Ekstrom, A. D. (2019). A Modality-Independent network underlies the retrieval of Large-Scale spatial environments in the human brain. *Neuron*, 104(3):611–622.e7.

Ishikawa, T., Fujiwara, H., Imai, O., and Okabe, A. (2008). Wayfinding with a GPS-based mobile navigation system: A comparison with maps and direct experience. *J. Environ. Psychol.*, 28(1):74–82.

Ishikawa, T. and Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: individual differences in the development of metric knowledge and the integration of separately learned places. *Cogn. Psychol.*, 52(2):93–129.

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., and Golledge, R. G. (1998). Spatial updating of Self-Position and orientation during real, imagined, and virtual locomotion. *Psychol. Sci.*, 9(4):293–298.

Lawson, B. D., Kass, S., Lambert, C., and Smith, S. (2004). Survey and review concerning evidence for gender differences in motion susceptibility. *Aviat. Space Environ. Med.*, 75(4):105.

Lessels, S. and Ruddle, R. A. (2005). Movement around real and virtual cluttered environments. *Presence*, 14(5):580–596.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., and Fry, P. A. (1993). Nonvisual navigation by blind and sighted: assessment of path integration ability. *J. Exp. Psychol. Gen.*, 122(1):73–91.

Münzer, S., Zimmer, H. D., and Baus, J. (2012). Navigation assistance: a trade-off between wayfinding support and configural learning support. *J. Exp. Psychol. Appl.*, 18(1):18–37.

Münzer, S., Zimmer, H. D., Schwalm, M., Baus, J., and Aslan, I. (2006). Computer-assisted navigation and the acquisition of route and survey knowledge. *J. Environ. Psychol.*, 26(4):300–308.

Nakamura, K., Kawashima, R., Sato, N., Nakamura, A., Sugiura, M., Kato, T., Hatano, K., Ito, K., Fukuda, H., Schormann, T., and Zilles, K. (2000). Functional delineation of the human occipito-temporal areas related to face and scene processing. a PET study. *Brain*, 123 (Pt 9)(9):1903–1912.

O'Craven, K. M. and Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stiimulus-specific brain regions. *J. Cogn. Neurosci.*, 12(6):1013–1023.

Patai, E. Z., Javadi, A.-H., Ozubko, J. D., O'Callaghan, A., Ji, S., Robin, J., Grady, C., Winocur, G., Rosenbaum, R. S., Moscovitch, M., and Spiers, H. J. (2019). Hippocampal and retrosplenial goal distance coding after long-term consolidation of a Real-World environment. *Cereb. Cortex*, 29(6):2748–2758.

Plechatá, A., Sahula, V., Fayette, D., and Fajnerová, I. (2019). Age-Related differences with immersive and non-immersive virtual reality in memory assessment. *Front. Psychol.*, 10:1330.

Qasim, S. E. and Jacobs, J. (2016). Human hippocampal theta oscillations during movement without visual cues. *Neuron*, 89(6):1121–1123.

Richardson, A. E., Montello, D. R., and Hegarty, M. (1999). Spatial knowledge acquisition from maps and from navigation in real and virtual environments. *Mem. Cognit.*, 27(4):741–750.

Riecke, B. E., Bodenheimer, B., McNamara, T. P., Williams, B., Peng, P., and Feuereissen, D. (2010). Do we need to walk for effective virtual reality navigation? physical rotations alone may suffice. In *Spatial Cognition VII*, pages 234–247. Springer Berlin Heidelberg.

Rolls, E. T. (1999). Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus*, 9(4):467–480.

Ruddle, R. A. and Lessels, S. (2006). For efficient navigational search, humans require full physical movement, but not a rich visual scene. *Psychol. Sci.*, 17(6):460–465.

Stangl, M., Kanitscheider, I., Riemer, M., Fiete, I., and Wolbers, T. (2020). Sources of path integration error in young and aging humans. *Nat. Commun.*, 11(1):2626.

Vasser, M. and Aru, J. (2020). Guidelines for immersive virtual reality in psychological research. *Current Opinion in Psychology.*

Vlček, K. and Laczó, J. (2014). Neural correlates of spatial navigation changes in mild cognitive impairment and alzheimer's disease. *Front. Behav. Neurosci.*, 8:89.

Waller, D. and Greenauer, N. (2007). The role of body-based sensory information in the acquisition of enduring spatial representations. *Psychol. Res.*, 71(3):322–332.

Waller, D., Hunt, E., and Knapp, D. (1998). The transfer of spatial knowledge in virtual environment training. *Presence: Teleoperators and Virtual Environments*, 7(2):129–143.

West, G. L., Drisdelle, B. L., Konishi, K., Jackson, J., Jolicoeur, P., and Bohbot, V. D. (2015). Habitual action video game playing is associated with caudate nucleus-dependent navigational strategies. *Proc. Biol. Sci.*, 282(1808):20142952.

Witmer, B. G., Bailey, J. H., Knerr, B. W., and Parsons, K. C. (1996). Virtual spaces and real world places: transfer of route knowledge. *Int. J. Hum. Comput. Stud.*, 45(4):413–428.

Zhang, H., Zherdeva, K., and Ekstrom, A. D. (2014). Different "routes" to a cognitive map: dissociable forms of spatial knowledge derived from route and cartographic map learning. *Mem. Cognit.*, 42(7):1106–1117.

List of publications

Hejtmánek, L., Starrett, M., Ferrer, E., Ekstrom, A. D. (2020). How Much of What We Learn in Virtual Reality Transfers to Real-World Navigation? *Multisensory Research*, 1–25. IF: 1.829

Vlček, K. , Fajnerová, I., Nekovářová, T., **Hejtmánek, L.**, Janča, R., Ježdik, P., Kalina, A., Tomášek, M., Kršek, P., Hammer, J., Marusič, P. (2020) Mapping the scene and object processing networks by intracranial EEG. *Frontiers in Human Neuroscience*, Accepted. IF: 2.673

Plechatá, A., **Hejtmánek, L.**, Fajnerová, I. (2020). Virtual Supermarket Shopping Task for cognitive assessment and rehabilitation of psychiatric patients: Validation in chronic schizophrenia. *Československá psychologie*, Accepted. IF: 0.373

Harootonian, S. K., Wilson, R. C., **Hejtmánek, L.**., Ziskin, E. M., Ekstrom, A. D. (2020). Path integration in large-scale space and with novel geometries: Comparing vector addition and encoding-error models. PLoS Computational Biology, 16(5), e1007489. IF: 4.700

Hejtmánek, L., Oravcová, I., Motýl, J., Horáček, J., Fajnerová, I. (2018). Spatial knowledge impairment after GPS guided navigation: Eye-tracking study in a virtual town. *International Journal of Human-Computer Studies*, 116, 15–24. IF: 2.300

Other publications

Hejtmánek, L., Fajnerová, I. (2019). Využití virtuální reality v psychiatrii. *Psychiatrie* , 23(4), 188–196.

Fajnerová, I., Oravcová, I., Plechatá, A., **Hejtmánek, L.**, Sahula, V., Vlček, K., Nekovářová, T. (2017). The virtual Episodic Memory Task: Towards remediation in neuropsychiatric disorders. *2017 International Conference on Virtual Rehabilitation (ICVR)*

Plechatá, A., Fajnerová, I., **Hejtmánek, L.**, Sahula, V. (2017). Development of a virtual supermarket shopping task for cognitive remediation of memory and executive functions in schizophrenia. *2017 International Conference on Virtual Rehabilitation (ICVR)*

Posters and talks

Brožka, H., Radostová, D., Alexová, D., **Hejtmánek, L.**, Stuchlík, A. (2020). Development of a Novel Incidental One-Trial Temporal Binding Task. *FENS*

Hejtmánek, L., Králová, M., Fajnerová, I. (2019). How does GPS visualization affect navigation performance? An eye tracking insight. *European Brain and Behaviour Society*

Hejtmánek, L. (2018). Enriched body-based cues and transfer to real-world environments. *Interdisciplinary Navigation Symposium*

Hejtmánek, L., Tomášek, M., Marusič, P., Vlček, K. (2017). Theta power modulation during egocentric and allocentric navigation in virtual and real environment. *International conference on cognitive neuroscience*