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The Effects of Expectancy and Control on the Perception of Ego-Motion in Space: a combined Postural and Electrophysiological Study.

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Zusammenfassung

Den Grundstein für diese Arbeit legte die Frage: spielt es für die Wahrnehmung und Verarbeitung von visuellem Feedback, das in Folge von Eigenbewegung im Raum entsteht, eine Rolle wie viel Kontrolle wir über die Bewegung haben? Wird das Feedback von aktiven Bewegungen anders verarbeitet als das von passiven? Im ersten Experiment explorierten wir die Möglichkeit uns dieser Fragestellung mit optic flow als visuellem Stimulus zu nähern. Wir haben dazu ein Experiment entwickelt bei dem gesunde Proband:innen unterschiedlich viel Kontrolle über den optic flow haben und sie anschließend zu ihrem Bewegungsempfinden (Vection) befragt. Während dieses Experiment keine relevante Modulation nachweisen konnte, so stellte es doch eine wichtige methodologische Grundlage für die Entwicklung der weiteren Experimente dar. Die wichtigsten Änderungen in Experiment 2 umfassten zum einen Modifikationen an den Stimuli und eine ausgeprägtere Formalisierung der Instruktionen, zum anderen die zusätzliche Erhebung von neurophysiologischen und posturalen Daten. Diese Änderungen erlaubten uns nicht nur explizite Unterschiede in der Intensität der Wahrnehmung von Vection zu erfassen, sondern auch eventuelle Modifikationen in der Verarbeitung der Stimuli messbar zu machen. Dieses Experiment lieferte Hinweise darauf, dass Stimuli mit denselben physikalischen Eigenschaften auf kortikaler Ebene anders verarbeitet werden, je nachdem ob sie selbst initiiert oder Computer-generiert sind. In Experiment 3 führten wir klassische Kontrollbedingungen wie zum Beispiel Versuche mit statischen Stimuli ein. Wir veränderten weiterhin die Körperposition, so dass Proband:innen nun saßen und die Hälfte der Versuche mit einer Kinnstütze stattfand. Damit konnten wir das Risiko, das unsere neurophysiologischen Effekte Bewegungsartefakte sind, minimieren. Insgesamt waren wir dazu in der Lage die Haupteffekte von Experiment 2 (agency-abhängige Modulation der evozierten Desynchronisation und der Amplitude der evozierten Potentiale) in Experiment 3 zu reproduzieren, obwohl wir hier eine deutlich größere Kohorte sowie andere Proband:innen in einer anderen Körperhaltung testeten. Diese Resultate sind sehr robust, so dass sie weiterhin deutlich erkennbar sind, auch nachdem wir versuchsweise die Hälfte der Proband:innen aus der Analyse ausgeschlossen hatten. Zusätzlich zu unserer ursprünglichen Fragestellung zeigten unsere Experimente, dass die wissenschaftliche Community mehr auf die Ergebnisse von Studien, die ein mobiles EEG-Setup verwenden, vertrauen kann, solange es sich um robuste Effekte handelt und ausreichend

auf die Identifikation und Entfernung von Bewegungsartefakten geachtet wird. Außerdem konnten wir mit unseren Daten dazu beitragen die Zusammenhänge zwischen Vection und visuell-induzierter Bewegungskrankheit besser zu verstehen.

Unsere Experimente versuchen die Brücke zu schlagen zwischen den jeweils für sich gesehen hoch relevanten Forschungsfeldern rund um die visuelle Bewegungswahrnehmung und den Sense of Agency. Diese Felder zusammenzubringen wird eine essenzielle Rolle spielen, sowohl um das volle Potential von VR-Applikationen zu entfalten als auch um Lokomotion und Navigation umfassender zu begreifen. Die Fähigkeit Eigenbewegung von Bewegungen in der Umgebung anhand von visuellen Informationen zu unterscheiden, ist entscheidend um in der komplexen, dynamischen Umwelt unseres täglichen Lebens erfolgreich agieren und navigieren zu können. Diese Fähigkeit ist ein schönes Beispiel für die dynamische Koppelung von Handlung und Wahrnehmung zum Erreichen unserer Ziele und vermutlich eine der fundamentalsten Fähigkeiten nicht nur für Menschen, sondern auch im übrigen Tierreich. Möglicherweise so fundamental, dass sie die evolutionäre Basis für die spätere Entwicklung des menschlichen Gehirns in all seiner Komplexität und Schönheit, gelegt haben könnte (Godfrey-Smith 2016).

Abstract

In the beginning of this work was the scientific question: does the amount of control over visual self-motion cues influence their processing and / or perception? In Experiment 1, we tried to explore the possibility to use optic flow as a visual motion cue and see whether we can observe a sensory attenuation or modulation on the behavioural level in trials in which the optic flow was self-initiated using putative different levels of control by instructed or uninstructed button-presses compared to passive flow. This experiment, while not able to demonstrate a sensory modulation and with several important limitations (see below), was however an important basis for the planning of Experiment 2 and a proof-of-concept that this method has the potential to address our research question and is feasible given our facilities. In Experiment 2, we tried to overcome some of the limitations, further improved the reproducibility (e.g. stimuli and instructions) and extended our methodology to the measurement of neurophysiological and postural data to enquire about not only the behavioural level but also the processing on the physiological level. This experiment presented evidence that self-motion cues with the same physical properties are somehow processed differently at the cortical level depending on whether they are self-initiated or not. In addition to overcoming certain limitations in Experiment 3 (e.g. having a no optic flow control condition and using the standard EEG setup besides the mobile setup from Experiment 2), we were able to reproduce our findings in different subjects, a larger population and under a different posture. We were also able to show that our results are highly robust (e.g. removal of half the participants from the analysis did not change the pattern). Further outcomes from our study are that the scientific community can put more trust into mobile EEG setups given robust effects and diligent artifact removal. Additionally, we contributed findings on the relationship of vection and VIMS and tried to bridge the gap between the highly relevant fields of research on visual motion perception and sense of agency. This might act as an exploratory foundation for further research which will be essential for the economical and medical applicability of VR devices and for a deeper understanding of locomotion and navigation per se. The ability to perceive self-motion cues and dissociate them from cues for motion in the environment is fundamental for being able to take actions in the complex, dynamic environments which are our daily lives. In fact, it could be seen as a classical example of the dynamic coupling of action and perception to reach goals which is one of the most fundamental abilities

not only for humans, but throughout the animal kingdom which may have lain the evolutionary basis for the later development of the human brain with its complexity as we see it nowadays (Godfrey-Smith 2016).

List of Abbreviations

AR	augmented reality
CSv	cingulate sulcus visual area
EEG	electroencephalography
ERD	event-related desynchronization
ERP	event-related potential
fMRI	functional magnetic resonance imaging
FoE	focus of expansion
IPS	Intraparietal sulcus
MS	Motion sickness
MST	Medial superior temporal area
MT	Middle temporal area
OF	Optic flow
SoA	sense of agency
VAS	visual analogue scale
VEP	visually-evoked potential
VIMS	visually-induced motion sickness
TMS	transcranial magnetic stimulation
VIP	ventral intraparietal sulcus
VIPR	visual-induced postural response
VR	virtual reality

“Perception is consequently an act that unfolds over time, rather than a momentary “percept” […]”

- William H. Warren in Perception of Space and Motion 1995

1. Introduction

1.1 Efference copies and the human motor control system

The function of the human motor control system is to allow us to navigate through and interact with our changing and often unpredictable environment safely (Frith, Blakemore et al. 2000, Bansal, Ford et al. 2018). The motor control system is thought to do this by regulating the interaction of motor commands and resulting sensory feedback in a dynamic way (e.g. online visual-guidance (Fajen 2021)) to be able to learn how to achieve our goals accurately and effectively; this requires learning from "mistakes", i.e. the mismatch between expected / desired results and actual results which is determined by the sensory feedback we perceive (Frith, Blakemore et al. 2000). One of the most famous examples of this process was introduced by Helmholtz (Von Helmholtz 1867): when we look forward and repetitively apply pressure on our eyelid, it appears as if the world was shaking. Helmholtz explained this phenomenon based on case studies of patients with ocular muscle palsy with the absence of direct sensory receptors to determine gaze direction (Bridgeman 2007); the brain therefore has to use a combination of the location of attended objects on the retinal image and integrate this information with efference copies of the motor commands of the eye muscles together with proprioceptive signals from eye muscles. However, when one fixates a target with the other eye closed while slowly applying pressure to the outer epicanthus, one will see that the gaze is still stable on the target while the visual world including the target appear to be moving. For Bridgeman, this is an argument against the interpretation by Helmholtz which implies that passive displacement of the eye which leads to movement of the retinal image in the absence of corresponding efference copies results in a mismatch which in turn is the cause for failing stabilization of the visual world (Bridgeman 2007); Bridgeman suggests that the successful fixation of the target can be seen as evidence that oculomotor control systems involved in the optokinetic reflex and smooth pursuit actually keep the retinal image stable. According to him, the apparent motion results from the efference copy generated by those active target fixation processes which in turn leads to a mismatch between the stable retinal image and the predictions based on the efference copy. While Helmholtz's theory mainly aimed at explaining this physiological phenomenon, the latter interpretation is an excellent example for how interconnected the sensorimotor system is and how perception is a

rather active performance instead of the mere interpretation of physical properties of the external world.

1.2 Motion perception and the visual system

Visual guidance during navigation

One of the reasons which make vision probably the most important sense for online guidance of locomotion in humans is that it gives us not only information about the position of the body in the environment (e.g. vestibular system and proprioception) but also relative to the surroundings and even about moving and stationary objects which are by now unrelated to us but might become relevant as they could be potential obstacles (e.g. walls) or goals (e.g. prey). One can describe ego-motion by dissociating it into its rotational and translational component which consist of 3 degrees of freedom each; all degrees of freedom except for translational velocity can be reconstructed from information on the retina (Festl, Recktenwald et al. 2012). More important aspects of the visual information we perceive are the spatial layout of our surroundings, object recognition (e.g. identity, shape, surface, object motion), dissociation between self- and object-motion and important cues for directing attention selectively e.g. by dissociating into task-relevant and -irrelevant information (even though many of those functions are probably supported by other sensory modalities) (Fajen 2021). The most common models trying to explain those processes are the model-based and the information-based approaches (Fajen 2021). The basic difference is that the information-based approaches only depend on currently available perceptual information to guide future actions (Zhao and Warren 2015) and therefore do not need to have a representation of the spatial layout and structure of the environment. For those approaches, more task-specific clues are sufficient to explain visual guidance processes e.g. to reach a moving target it is enough to always keep the visual angle stable while moving (as long as one assumes that the eyes look straight ahead) while information about the exact speed and distance of the target is redundant (Fajen 2021). On the other hand, model-based approaches contain more information and need to be updated regularly while having the clear advantage that the internal models also can be used to estimate the position of the target when important perceptual information is temporarily absent e.g. when the target is transiently hidden behind an obstacle (the precision however wanes over time) (Fajen 2021). The idea behind model-based approaches is

that currently available perceptual information is integrated with prior knowledge to form internal representations and/or models of the environment which are kept updated; those models then guide future actions (Loomis and Beall 2004). While the concept of internal models is now widespread in cognitive neuroscience and beyond (for general discussion of internal models and their applications in biology see (McNamee and Wolpert 2019)), it was first introduced by Craik in the early 1940s in his work "The nature of explanation" (Craik 1943) and can be described as an internal simulation of the external world (Fajen 2021). Zhao and Warren discuss both approaches and suggest that specific off-line tasks such as the blind walking task (being shown a target and then navigating to it without online visual input) probably require internal models while the putatively cheaper (in terms of cognitive demand) online action control is favoured whenever online (visual) information is available (Zhao and Warren 2015). To return to the earlier point, Fajen pointed out that active movement and exploratory behaviour is needed to be able to learn our own body dimensions and action capabilities, especially in situations with altered dimensions (Fajen 2021). This system is so useful because every movement we make has immediate sensory consequences (Frith, Blakemore et al. 2000). Humans are thus able to learn to react with the appropriate action in various different contexts and can adapt fast to changing contextual information (Frith, Blakemore et al. 2000). Electroencephalography (EEG) studies in infants suggest that children learn to rely on and interpret optic flow information when they start to locomote and actively explore their environment (Agyei, Holth et al. 2015, Rasulo, Vilhelmsen et al. 2021). Aged 4-6 months, their mechanisms for global integrating of motion information are still immature (Hou, Gilmore et al. 2009); in fact prelocomotor infants seem to be unable to differentiate between different optic flow speeds (Rasulo, Vilhelmsen et al. 2021). Even in children aged 6-12 years studies have shown different motion processing and speed estimation compared to adults (Rasulo, Vilhelmsen et al. 2021) suggesting continuous ongoing development. This learning involved in neurodevelopment could be driven by updating our internal models e.g. via the above mentioned continuous mismatch minimization (Frith, Blakemore et al. 2000).

Visual motion perception and optic flow

Optic flow consists of the sum of information contained in the visual array resulting from the relative motion between an observer and their surroundings (Uesaki and Ashida 2015) and with this information on the relative movement of objects in the visual

field from the perspective of the observer (Vilhelmsen, van der Weel et al. 2015). The general idea is that objects which are nearer to the moving observer cover a greater distance per time (in the visual field and on the retina as well) compared to objects further away. The specific acceleration pattern of the individual objects in relation to each other can be used as a dynamic depth cue as it results in systematic changes of the retinal image (Fajen 2021). The term optic flow was first used during the 1940s by Gibson (Gibson 1950) during his work with military pilots of the Air force while the phenomenon per se was first described by the German scientist Hermann von Helmholtz in the 19th century (Von Helmholtz 1867). The most natural type of optic flow we perceive during daily life is the radially expanding pattern which accompanies forward translational movements (Crowell, Banks et al. 1998, Diels and Howarth 2013). This type of optic flow contains important features like acceleration towards the periphery of the visual field and motion parallax (Yantis 2013) and can be defined by its physical properties such as the direction which is determined by its focus of expansion (FoE, the static point in the visual field from which every object is diverging), the coherence in the pattern (e.g. all objects moving in a way which matches a moving observer in a static environment) and the speed of expansion (which is normally increasing towards the periphery (Fajen 2021). Those features can be used as cues for self-motion perception which ultimately help with avoiding obstacles, capturing objects and estimating the time-to-contact which in turn can be used to prepare for impacts (Fajen 2021). Parry and Micklewright demonstrated the importance of optic flow for distance estimation in a fascinating study which showed that even though participants ran the same distance with the same speed and had motion information from other senses available, they felt less physical exertion when viewing optic flow suggesting a slower pace (Parry and Micklewright 2014). Self-motion perception is said to consist of three distinct phenomena: 1. the perceived heading direction, 2. vection (definition see below), and 3. required postural adjustments (Warren 1995).

Heading direction estimation

The heading can be estimated, in the case of smooth forward motion, by the identification of the FoE (Gibson 1950). This mechanism is actually pretty accurate during isolated translational motion given that the brain is able to determine the heading with an accuracy of 1°-2° of visual angle just by using optic flow as a cue without the need for oculomotor efference signals, multiple fixations or edge parallax (W. H. Warren & Hannon, 1988). During exposure to optic flow consisting of combined translational and

rotational components, the FoE does not correspond to heading but rather to the fixation point (Fajen 2021). While there are also other retinal and extra-retinal heading direction cues (especially needed when not confronted with purely translational components), this estimation from optic flow can already be sufficient to guide goal directed navigation by moving in such a way that the FoE is directly on the goal and avoid hitting static objects like two parking cars with an opening between them (Gibson 1950, Fajen 2021): an observer just needs to make sure that the distance of the car on the right and on the left of the FoE stays aligned while moving forward. It must be pointed out however that other concepts, independent of optic flow, like e.g. egocentric reference frames could also enable the observer to solve the same task (Fajen 2021). In most real-life situations, interpretation of the information contained in the visual array is harder as either other objects in the environment are also moving independently of ourselves or our eyes might move (Warren 1995) which impairs the global coherence of the optic flow and can even hide the FoE (Fajen 2021), which interestingly compromises us little in daily life, but biases in heading judgments can be observed in laboratory settings (Layton and Fajen 2016). A possible explanation why we have relatively few problems with solving such more complex tasks in real life is that we can also use extra-retinal information such as efference copies and feedback afference and integrate those with retinal information about self-motion to generate predictive forward models to guide locomotion using an egocentric reference frame (Rushton, Chen et al. 2018). Another important concept putatively used by our (visual) motion processing system is ‘flow parsing’, namely filtering out the components of the perceived optic flow which are attributable to self-motion to isolate object motion in the environment (for an overview of the involved brain structures see (Pitzalis, Serra et al. 2020)). This information can then be used to e.g. avoid collisions (Warren and Rushton 2007). While Warren and Rushton demonstrated that flow parsing can be done based on visual information alone, newer studies suggest that it is essentially a multisensory process which also depends on or is at least influenced by non-visual information (Fajen and Matthis 2013). For the rationale of our study, it is important to stress that the physical properties of the perceived optic flow can be similar or even identical independently of whether the observer is actively navigating, passively displaced or stationary with a moving environment (Durgin, Gigone et al. 2005). However, heuristics like the empirical knowledge that surroundings tend to be stationary in everyday life, can be used as

a reference for spatial configuration (Mergner, Schweigart et al. 2005) and multisensory information, as also used for flow parsing, can help in differentiating those distinct situations (Bansal, Ford et al. 2018, Brooks and Cullen 2019). Phenomena like flow parsing can be seen as evidence that (visual) perception is an active and dynamic process which is influencing action control in real time or as Fajen puts it: “[B]ehavior is emergent rather than planned in advance. Actors do not follow a predetermined trajectory; rather, the trajectory emerges in real time as locomotion is regulated based on currently available information.” (Fajen 2021).

1.3 Sensory modulation

The earliest reports can be traced back to Charles Darwin’s “The expression of the emotions in man and animals“, where he reflected on the question why “a child can hardly tickle itself” (Darwin 1872) and von Helmholtz observed in his “Handbuch der physiologischen Optik” that the brain needs to cancel out the optic flow produced by eye movements to allow for perceptual stability (Von Helmholtz 1867). While the mechanism responsible for visual stabilization is probably other than previously thought (Bridgeman 2007), von Holst and Mittelstädt further refined the concept developed by Helmholtz when they introduced ‘efference copies’ which give rise to forward models (for an overview of forward models see (Pickering and Clark 2014)) in their important work “Das Reafferenzprinzip” (von Holst and Mittelstaedt 1950). Throughout the last decades, evidence has accumulated that stimuli with the same physical properties can be processed and / or perceived differently based on whether they are self-generated or externally-generated; this has been shown in the somatosensory (Weiskrantz, Elliott et al. 1971, Claxton 1975, Blakemore, Wolpert et al. 1998, Blakemore, Frith et al. 1999, Blakemore, Wolpert et al. 1999, Sukhwinder S. Shergill, Gabrielle Samson et al. 2005), auditory (Bäß, Jacobsen et al. 2008, Baess, Horváth et al. 2011, Weiss, Herwig et al. 2011, Desantis, Weiss et al. 2012, Hughes, Desantis et al. 2013, Timm, SanMiguel et al. 2013, Reznik, Henkin et al. 2015, Straube, van Kemenade et al. 2017, Kaiser and Schütz-Bosbach 2018), visual (Cardoso-Leite, Mamassian et al. 2010, Gentsch and Schütz-Bosbach 2011, Hughes and Waszak 2011, Straube, van Kemenade et al. 2017) and vestibular domain (Howard, Zacher et al. 1998, Cullen and Minor 2002, Cullen and Roy 2004, Sadeghi, Minor et al. 2007, Jamali, Sadeghi et al. 2009, Brooks and Cullen 2019) and it has been suggested that it might rely on general modality-

independent mechanisms (Gentsch and Schütz-Bosbach 2011, Straube, van Kemenade et al. 2017). The underlying idea is that actions by the observer lead to expected and therefore predictable sensory feedback or sensory consequences. Those consequences can be predicted by the observer based on self-specific information (Weiss, Herwig et al. 2011) like motor-commands or general predictive mechanisms (Kaiser and Schütz-Bosbach 2018); disentangling those two possible mechanisms is not trivial and requires specifically designed experiments (Levine, Stern et al. 2014, Press, Kok et al. 2020). The existence of such predictions has several advantages; to name just a few: they can be used to compare expected from actual outcome to allow adjustments in sensorimotor learning (Bansal, Ford et al. 2018), they can be used to cancel out the expected sensory consequences to reduce processing load (Frith, Blakemore et al. 2000, Press, Kok et al. 2020), in processes such as flow parsing (see above) or more abstract processes, to be able to attribute authorship of actions (Frith, Blakemore et al. 2000) which might have important implications as the foundation for our moral philosophy and attribution of responsibility (Synofzik, Vosgerau et al. 2008, Haggard 2017).

1.4 Differences between active and passive ego-motion

Specifically relevant for our studies is the question whether there is evidence for the presence of sensory modulation of motion perception during active compared to passive self-motion. This has been studied by comparing e.g. active with passive head turns in humans (Blouin, Labrousse et al. 1998) demonstrating improved spatial precision following active head turns and in monkeys (Cullen and Roy 2004) showing that while the afferent vestibular information was physically identical and led to almost the same signal on the level of the vestibular organs, it is already modulated on the level of the vestibular nuclei and processed differently upstream.

As suggested by Patrick Haggard, it can be expected that effects of agency can be extended to VR (Haggard 2017). And indeed, another line of research compared actively navigating in virtual environments to watching the replay of this journey or driving simulator race (Dong, Yoshida et al. 2011, Havranek, Langer et al. 2012). Dong et al. found that drivers swayed more in total, and their sway was more predictable while they experienced less motion sickness compared to the participants who just watched the replay (Dong, Yoshida et al. 2011). Havranek et al. observed that participants'

sense of presence in the virtual environment was judged to be higher when they navigated actively (Havranek, Langer et al. 2012). Additionally, Durgin et al. reported that participants who are actively walking while exposed to radially-expanding optic flow, experience the flow as slower than when they were horizontally displaced in the same way (Durgin, Gigone et al. 2005). Furthermore, Riecke and Feuereissen showed that 3D visual spatial structure was perceived differently by actively compared to passively moving observers (Riecke and Feuereissen 2012). Levine et al. observed that the motion-induced nausea and gastric arrhythmia, both common symptoms of motion sickness, were reduced when participants had a higher level of control over the optokinetic drum around them (Levine, Stern et al. 2014). Besides, Oman suggested that adaptation to motion sickness eliciting stimuli is easier and faster when subjects are voluntarily moving compared to passive movements even though adaptation also occurs in experiments with e.g. passive head-movements (Oman 1990).

1.5 Vection

The second aspect of self-motion perception according to Warren is vection (Warren 1995). The exposure to optic flow can be used to induce vection even in stationary observers (Brandt, Wist et al. 1971). The term vection is generally used to describe the compelling subjective experience of ego-motion in space (Palmisano, Allison et al. 2015, Berti and Keshavarz 2020). Over the years, different definitions have been used either limiting vection to the visual domain or more broadly, to the experience of ego-motion in otherwise stationary subjects or as the accompanying experience in normal locomotion and treating it either as a perceptual illusion or as a normal physiological experience. Palmisano et al. identified the four most commonly applied definitions which will be presented in the following section (Palmisano, Allison et al. 2015); it must however be kept in mind, that the dissociation in illusion and normal physiological experience might be artificial as the visual stimulation might be identical in both cases and it would only truly be an illusion if there is exclusively environmental motion present (Dichgans and Brandt 1978).

1. Visual illusion of self-motion in physically stationary observers (Dichgans and Brandt 1978):

The main features of this definition are that vection is treated as an illusion, mainly elicited by using more or less naturalistic visual stimuli in otherwise stationary subjects. The classical example would be the drum with black and white stripes which is rotating around a standing or seated observer inducing circular vection which is subjectively not distinguishable from chair rotation (Brandt, Wist et al. 1971).

2. Illusion of self-motion in physically stationary observers:
This definition broadens the usage of the term vection to the subjective experience of ego-motion in stationary observers as induced by any type of sensory stimulation or a combination of different senses. However, the experience is still treated as illusory. Easy to imagine are examples like vestibular vection (a very uncommon term), e.g. induced by caloric (Fischer and Wodak 1924, Fasold, von Brevern et al. 2002) or galvanic (Cress, Hettinger et al. 1997, Lepecq, Waele et al. 2006) vestibular stimulation, auditory vection, e.g. simulating approaching or diverging from a sound source (Dodge 1923, Lackner 1977, Sakamoto, Osada et al. 2004, Riecke, Feuereissen et al. 2008, Väljamäe 2009, Keshavarz, Hettinger et al. 2014); haptokinetic vection, e.g. applying tactile motion stimuli to large enough areas of the body or modulate the pressure on the feet (Dichgans and Brandt 1978, Nilsson, Nordahl et al. 2012, Nordahl, Nilsson et al. 2012, Murata, Seno et al. 2014); proprioceptive or arthrokinetic vection, e.g. passive rotation of participants limbs (Brandt, Büchele et al. 1977, Howard, Zacher et al. 1998); biomechanical vection, e.g. aftereffects after prolonged time on a treadmill (Bles 1981, Riecke, Feuereissen et al. 2011).

3. Visual mediated perception of self-motion:
This definition is mostly used for more complex congruent or incongruent combinations of physical motion and visual self-motion cues which would not fall under either definition #1 or #2 (Palmisano, Allison et al. 2015). Some examples include e.g. passive whole body motion with optic flow (Wright, DiZio et al. 2005), active head motion with more or less congruent visual motion displays (Kim and Palmisano 2008, Kim and Palmisano 2010, Ash, Palmisano et al. 2011, Ash, Palmisano et al. 2011), abstract, highly artificial situations such as standing subjects performing breaststroke movements as if they would be swimming (Seno, Funatsu et al. 2013), walking on the spot (Palmisano, Allison et al. 2014) or on a treadmill (Onimaru, Sato et al. 2010, Seno, Ito

et al. 2011, Ash, Palmisano et al. 2013, Palmisano, Allison et al. 2014) or full physical motion in VR environments (Riecke, Feuereissen et al. 2012).

4. Conscious subjective experience of self-motion:
This is the broadest vection definition which includes subjective self-motion perception elicited from both illusory and real motion, by any type of sensory stimulation. This definition can be applied for studying the qualia of self-motion perception but also includes definitions #1-3. Subtypes could be called e.g. active vection i.e. the visual feedback resulting from active locomotion in a well-lit environment, passive vection i.e. the visual input one perceives while being a passenger sitting next to the driver in a car or stationary vection i.e. the classical study with participants standing or sitting in front of a screen which shows optic flow (Palmisano, Allison et al. 2015).

Typical time course of vection onset

Following those different definitions and over the course of the almost 100 years that vection has been studied now, various different study designs have been successful in inducing some type of self-motion perception with different intensities and onset latencies (Palmisano, Allison et al. 2015). It is typically observed that vection in the laboratory setting does not start immediately but takes some time to build up (Riecke and Feuereissen 2012), while real life examples like the train-illusion are striking in their intensity almost immediately after motion onset (Riecke 2006). The typical time course includes a phase of purely object-motion perception (objects in the external world seem to be moving), a transitional phase of combined self- and object-motion perception, followed by a phase of isolated self-motion perception (Palmisano and Riecke 2018). Palmisano et al. remarked that while vection is much more commonly studied and relevant nowadays, it is often less compelling and takes longer to begin because of the usage of smaller computer generated displays (Palmisano, Allison et al. 2015) compared to room-tilts (Lee and Lishman 1975, Bles, Vianney de Jong et al. 1983) or full-body rotating drums (Brandt, Wist et al. 1971). A wide range of vection latencies can be found in the literature: from at least 1 to 2 s (Berthoz, Pavard et al. 1975, Warren 1995), over the most commonly reported 1 to 10 s (Dichgans and Brandt 1978, Palmisano, Allison et al. 2015, Palmisano and Riecke 2018) or 2 to 30 s (Riecke, Schulte-Pelkum et al. 2006, Riecke and Feuereissen 2012), up to ranges of 0.46 to 40 s (Seno, Sawai et al. 2017, Seno, Murata et al. 2018). In line with the remark by

Palmisano et al. (Palmisano, Allison et al. 2015), Riecke suggested that vection onset latency might be a measure for the vection inducing capability of the stimuli (Riecke 2006). It has been proposed that this might be the critical factor for increasing immersion in VR environments, especially for settings which do not allow free full physical motion e.g. on motion platforms or treadmills. In a 2006 study, Riecke reported some trials with almost immediate vection onset using motion cueing with wheelchairs (Riecke 2006) which the same group however was not able to reproduce using game chairs (Riecke and Feuereissen 2012).

Functional significance

Berti and Keshavarz suggested that vection may be important for behavioural adaptation in dynamic environments and goal-oriented behavioural control because it could be one of the signals involved in processing motion related information and in dissociating object-motion in the environment from self-motion (Berti and Keshavarz 2020). Furthermore, Kovács et al. hypothesized that a function of vection might be to abolish the adaptation in the neural response following repetitious exposure to the same stimulus (Grill-Spector, Henson et al. 2006); this might allow us to keep track of the visual cues after the veining of vestibular input during exposure to e.g. continuous forward motion as during long car rides on empty highways (Kovács, Raabe et al. 2007); the vestibular system seems not to be able to differentiate between moving with a constant velocity and being stationary because the hair cells in the inner ear are only sensitive to acceleration (Dichgans and Brandt 1978). Possible applications of vection to increase the effectiveness of virtual reality devices are discussed below.

Cognitive influence on vection perception

In recent years it has become clearer that the vection inducing capability of a setup is not only dependent on the bottom-up physical properties of the stimuli e.g. luminescence, dot number/density, global coherence, depth cues, size of the field of view, etc. (Brandt, Dichgans et al. 1973, Berthoz, Pavard et al. 1975, Brandt, Wist et al. 1975, Dichgans and Brandt 1978, Allison, Howard et al. 1999, Riecke 2010, Keshavarz, Philipp-Muller et al. 2019) but also on top-down cognitive influence e.g. plausibility of self-motion in the setting, priming of expectations, attention paid to the stimuli, how photorealistic the visual scene is, different personality traits, etc. (Kitazaki and Sato

2003, Schulte-Pelkum, Riecke et al. 2003, Riecke, Schulte-Pelkum et al. 2006, Riecke 2010, Palmisano, Allison et al. 2015, Berti and Keshavarz 2020, D'Amour, Harris et al. 2021). While those cognitive factors offer opportunities, both from the fundamental research perspective, with the aim to learn more about the subjective experience of humans but also as a possible tool to increase the applicability for e.g. clinical applications of VR, they also pose an inherent problem for the interpretation of the subjective intensity judgments of subjective phenomena such as vection (Palmisano, Allison et al. 2015, Berti and Keshavarz 2020). It would therefore be useful to have objective markers of vection to know when the participants experience it without having them to report it explicitly. As Berti and Keshavarz pointed out, the ideal objective marker would be e.g. an EEG, positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) signature that is selectively present during self-motion perception and completely absent during object-motion while furthermore being highly reproducible, ideally on a trial-by-trial basis (Berti and Keshavarz 2020).

1.6 Postural and neurophysiological correlates

Neurophysiological correlates of vection and optic flow

One of the first studies to attempt this, found differences in the brain activity on the level of individual participants but no common pattern across their five participants (Tokumaru, Kaida et al. 1999). Kleinschmidt and colleagues (Kleinschmidt, Thilo et al. 2002) found a deactivation in early motion-sensitive visual areas and vestibular parieto-insular cortex (PIVC) during circular vection (compared to the exposure to the same stimuli without the experience of vection), however no change in known higher-order motion-sensitive optic flow reactive areas in temporal and parieto-occipital cortex with the medial superior temporal area (MST) and V5a was observed while they showed transient activation during perceptual switching. Deutschländer et al. showed bilateral activations in visual cortices, parieto-occipital motion sensitive areas, MT/V5, intraparietal sulcus (IPS), right precuneus as well as precentral and middle temporal gyri in their PET study during linear- and roll-vection (Deutschländer, Bense et al. 2004). It must be noted that a bistable percept such as vection (Kleinschmidt, Thilo et al. 2002) has the problem that the temporal resolution is a critical factor in the interpretation of fMRI and PET results and it might not always be easy to safely discriminate between (de-)activation during object-motion, vection, the transitional phase or just the

moment when the percept switches even if one does not consider the inevitable temporal delay due to reporting of a subjective phenomenon. For an overview of regions which have been shown to be involved in vection experience in fMRI studies see the comprehensive review by Berti and Keshavarz (Berti and Keshavarz 2020); the most important regions seem to be the medial motion area V6 (Kovács, Raabe et al. 2007), the MT+ complex including the middle temporal area MT/V5 and the MST, the ventral intra-parietal area (VIP) and intra parietal sulcus motion area (IPSmot), the cingulate sulcus visual area (CSv), extra-striate V3 accessory area (V3A) and the posterior insular (vestibular) cortex (PIVC/PIC) (Pitzalis, Sdoia et al. 2013, Berti and Keshavarz 2020). The MT+ complex is known to respond to optic flow stimuli and receive extra-retinal input i.e. vestibular signals and motor commands (Morrone, Tosetti et al. 2000, Kovács, Raabe et al. 2007), which has also been shown using single-cell recordings of MSTd cells in monkeys (Angelaki, Gu et al. 2011, Gu, DeAngelis et al. 2012); in fact, microstimulation of those cells was able to bias heading judgement based on visual information and less pronounced also on vestibular information (Gu, DeAngelis et al. 2012). Therefore, according to the sensory conflict theory, it is likely that this region is involved in suppression of the vestibular signals to eliminate the visuo-vestibular conflict; interestingly, it seems that the visuo-vestibular interaction might be different for rotational and translational vection with the need for a stronger suppression of the vestibular input during rotational vection (Kovács, Raabe et al. 2007). Based on data and observations by Nishiike et al. and a few years later by Indovina et al. (Nishiike, Nakagawa et al. 2002, Indovina, Maffei et al. 2005), Uesaki and Ashida suggested that the usage of accelerating stimuli might lead to robust PIVC activation and thus to a strong visuo-vestibular interaction in the form of a co-activation which might be the neurophysiological correlate of the vestibular system supporting the visual system in the interpretation of ‘arbitrary’ accelerating stimuli (Uesaki and Ashida 2015) in which it is thought not to be highly proficient as an isolated sense given its preference for constant velocity motion (Indovina, Maffei et al. 2005). In general, there seems to be a considerable overlap of brain areas which are traditionally considered to be ‘vestibular’, visual self-motion perception areas (Britton and Arshad 2019) and the so called dorsal stream (Kravitz, Saleem et al. 2011).

Kovács et al. (Kovács, Raabe et al. 2007) found, using fMRI, that MT+, precuneus, bilateral dorsal parts of intraparietal sulcus and the left posterior IPS were all more active in trials in which subjects reported to perceive rather linear vection than object-

motion; activations in those regions were however not vection selective. This problem is quite common as it is inherently hard to identify any regions which are specifically active during visual self-motion perception but not during object-motion perception. Most of the aforementioned studies demonstrate only decreased or increased activity during vection perception. If one takes a closer look into the brain areas involved in processing of optic flow one will find a huge overlap. Smith et al. for example used fMRI to show that MST and MT respond differently to changes in the global structure of optic flow (Smith, Wall et al. 2006); however they are both activated during exposure to the different types of optic flow. In the electrophysiological domain, Thilo et al. found a reduced P70 amplitude to pattern reversals during circular vection compared to object-motion over occipital channels (Thilo, Kleinschmidt et al. 2003). Also looking at event-related potentials (ERPs), Keshavarz, Berti and colleagues found an increase in the amplitude of the N2 component in the conditions which elicited most vection (Keshavarz and Berti 2014, Berti, Haycock et al. 2019), while Wei et al. showed that subjects with higher susceptibility to visually-induced motion sickness (VIMS) react with a stronger increase in the N2 component from incoherent to coherent visual flow compared to a low susceptibility group (Wei, Okazaki et al. 2019). In fact, Berti and Keshavarz presented the idea that this modulation of early ERP components might reflect a sensory feedback loop involved in the generation of the conscious aspect of the subjective percept of self-motion (Berti and Keshavarz 2020). Vection inducing stimuli are known to elicit stronger activation in areas such as MT+ and V6, multisensory VIP and vestibular PIVC (Uesaki and Ashida 2015) which is compatible with studies which identified an extra-striate dipole in temporo-parieto-occipital cortex to be the source for the N2 component (Probst, Plendl et al. 1993, Hollants-Gilhuijs, De Munck et al. 2000) and results by Tootell et al., demonstrating that the human MT behaves very similar to the much-studied macaque MT (Tootell, Reppas et al. 1995). Using transcranial magnetic stimulation (TMS), Stevens et al. have been able to show the causal involvement of V5/MT in global motion perception (Stevens, McGraw et al. 2009); a single TMS pulse given at around 130 - 150 ms after global motion onset which corresponds to the motion sensitive negativity (Agyei, Holth et al. 2015) or N2 component in the VEP elicited by optic flow (Maruyama, Kaneoke et al. 2002, Heinrich 2007) with a latency of approximately 130 - 150 ms after optic flow onset in adults (van der Meer, Fallet et al. 2008) and around 250 ms in young children (Vilhelmsen, van der Weel et al. 2015, Rasulo, Vilhelmsen et al. 2021), putatively disrupted integration

of motion signals (Sack, Kohler et al. 2006, Stevens, McGraw et al. 2009). Kovács et al. also suggested that the visuo-vestibular interaction can be dissociated during translational and rotational vection with a stronger focus on vestibular suppression during rotational vection which would explain the different findings from their study compared to the ones mentioned above using rotating stimuli (Kovács, Raabe et al. 2007). Additionally, Nishiike et al. proposed that sudden accelerating visual stimulation in the absence of vestibular stimulation leads to co-activation of visual areas and the PIVC in the left-hemisphere, thereby avoiding the conflict (Nishiike, Nakagawa et al. 2002). In line with the regions of interest from Kovács et al. (Kovács, Raabe et al. 2007), Wiest et al. presented the case of a 16 year old patient with epileptic seizures due to a ependymoma and repetitive “attacks” of linear self-motion perception with a focus in the right paramedian precuneus (Wiest, Zimprich et al. 2004). Direct electrical stimulation of this region was able to induce a vection sensation in the patient further highlighting the role of this area in the physiology of vection. Another important feature of the exposure to optic flow in EEG studies is a suppression of neural oscillations over parieto-occipital cortex, reflected by event-related desynchronization (ERD) in the alpha-band (Ehinger, Fischer et al. 2014, Vilhelmsen, van der Weel et al. 2015, Palmisano, Barry et al. 2016, Gramann, Hohlefeld et al. 2021). This ERD was found to be stronger during the experience of vection in depth (Barry, Palmisano et al. 2014, Palmisano, Allison et al. 2015). However, a similar ERD can also be observed due to vestibular or kinaesthetic stimulation (Ehinger, Fischer et al. 2014, Gale, Prsa et al. 2016). In general, it seems that changes in the alpha band (Tokumaru, Kaida et al. 1999, Dowsett, Herrmann et al. 2020, Harquel, Guerraz et al. 2020, McAssey, Dowsett et al. 2020) (especially over parieto-occipital channels, in line with the fMRI findings mentioned above), may be the most promising candidates for the identification of a neural correlate of vection (Berti and Keshavarz 2020). Alpha oscillations in the frequency band 8-13 Hz are thought to reflect phases of high- and low cortical excitability (Klimesch, Sauseng et al. 2007) and high local cortical alpha is generally associated with selective inhibition of processing of task-irrelevant information (Klimesch, Sauseng et al. 2007, Jensen and Mazaheri 2010) while ERD in the alpha-band has been interpreted as disinhibition (Edwards, Guven et al. 2018) or the end of modulatory effects of the functionally more important alpha oscillations (Klimesch, Sauseng et al. 2007).

1.7 Modulation of objective markers

Modulation of neurophysiological correlates during active motion control

While the alpha-band has been presented as an important possible neurophysiological correlate of vection, it is also thought to be involved in the modulation of cortical processing via processes such as expectancy and predictions (Harris 2005); a possible mechanism for how this modulation might take place is via phase re-alignments to prepare the brain for the processing of expected stimuli; this might be done by achieving specific alpha phases at the time when the afferent input reaches the cortex which can facilitate and ameliorate processing of those stimuli (Barry, Rushby et al. 2004). Gramann et al. suggested in line with these thoughts that the parieto-occipital ERD might reflect the mismatch between predictions and actual sensory feedback (Gramann, Hohlefeld et al. 2021); the underlying topic is discussed in more depth in the "Sensory modulation" sub-chapter. Page and Duffy showed a modulated response in stationary macaque monkeys' MSTd when they were actively controlling optic flow compared to viewing the same visual flow passively (Page and Duffy 2007) and Kovács et al. found a stronger activation of the left anterior cingulate cortex during active driving compared to viewing the same scene passively (Kovács, Raabe et al. 2007) which was in line with findings of one of the first functional imaging studies to compare active and passive movements: Weiller et al. found a selective activation of the cingulate gyrus during active movements using regional blood flow measures with $H_2{}^{15}O$-PET (Weiller, Jüptner et al. 1996).

Postural adjustments during exposure to optic flow and vection experience

Another often suggested objective marker for vection experience is related to postural regulation (Palmisano, Allison et al. 2015). It is known that human upright stance is controlled by the integration of input from different sensory modalities such as vision, the vestibular system, somatosensory input, and proprioception (Lishman and Lee 1973, Berthoz, Pavard et al. 1975, Mergner, Schweigart et al. 2005, Fujimoto and Ashida 2020). Therefore, it is not surprising that visual stimulation can lead to postural responses (Lee and Lishman 1975, Lestienne, Soechting et al. 1977, Dichgans and Brandt 1978). One important difference between vestibular and visual stimulation is that each vestibular signal must lead to postural adjustments while visual information must first be interpreted as either self- or environmental motion because only self-mo-

tion requires postural adjustments (Paulus, Straube et al. 1984). Furthermore, following Paulus et al. based on work by Kapteyn et al., there is evidence that motion perception and visual control of posture can be dissociated because it is possible to influence posture without the need for the experience of subjective motion perception (Kapteyn, Bles et al. 1979, Paulus, Straube et al. 1984). In general, it seems that the weighting of the different sensory modalities is dynamic with vision influencing posture more during an active motion task (Berthoz, Lacour et al. 1979) and with postulated visual dominance in VR (Fujimoto and Ashida 2020). Further evidence for the important role of vision comes from studies demonstrating that visual stimulation can modulate muscle activity in the legs with a time lag of only 100 ms (Nashner and Berthoz 1978, Berthoz, Lacour et al. 1979). In general, while the appropriate setup using the right visual stimuli can induce postural readjustment in (almost) all subjects, albeit with a high inter-individual variability (Lestienne, Soechting et al. 1977), participants tend to sway quite consistently in the opposite direction of the perceived self-motion direction (Lishman and Lee 1973, Lee and Lishman 1975, Lestienne, Soechting et al. 1977, Berthoz, Lacour et al. 1979, Fushiki, Kobayashi et al. 2005, Fujimoto and Ashida 2020), at least when standing while it seems that people show the reverse pattern when sitting (Fujimoto and Ashida 2020). The beginning of the postural response follows the onset of the visual stimulation almost immediately (Lestienne, Soechting et al. 1977, Fujimoto and Ashida 2020). Similar to motion sickness susceptibility, Brandt et al. demonstrated that the visual irritability is largest between the second and fifth year of life and afterwards decreases until it reaches the level of adults at around age 15 (Brandt, Wenzel et al. 1976). Adults still visibly swayed to their stimulation but had no relevant risk for falls. This is in line with findings by Paulus et al. showing that reduced visual acuity increases postural instability measurably but clinically non-relevant or without influencing postural control in daily life negatively (Paulus, Straube et al. 1984). Fushiki et al. demonstrated that vection onset during their optic flow trials led to an increase in postural instability (Fushiki, Kobayashi et al. 2005) and Kuno et al. showed that changes in vection are correlated with visual induced postural sway (Kuno, Kawakita et al. 1999). Palmisano et al. were able to predict the individual smooth vection strength of subjects by determining the reliance on visual information for postural control by comparing baseline sway with eyes open and eyes closed (Palmisano, Apthorp et al. 2014). Guerraz et al. showed that having active control over the visual scene led to reduced

postural responses compared to the presentation of the same but unexpected stimuli (Guerraz, Thilo et al. 2001).

1.7 Motion Sickness

Classical Motion Sickness

Motion sickness, with dizziness, discomfort, drowsiness, repetitive yawning, (cold) sweating, facial pallor, (migrainous) headache, bradycardia, increased salivation, sensation of bodily warmth, arterial hypotension, vomiting, apathy, loss of appetite, increased odour sensitivity and sopite syndrome (drowsiness, fatigue, mood changes) as the typical symptoms (Golding and Gresty 2015, Bertolini and Straumann 2016), was first described by the renowned Greek physician Hippocrates of Kos, more than 2000 years ago: “[S]ailing on the seas proves that motion disorders the body” (Bertolini and Straumann 2016). In those times boats offered one of the few environments where adults were confronted with passive motion stimuli. A common situation however which has to the best of our knowledge, not been studied yet, is infants being carried on the back of their mothers. This might not have been well studied, as it is often assumed that motion sickness susceptibility below the age of two is very low (Reason and Brand 1975, Bowins 2010) which might not be true for very young children with vestibular disturbances (Lipson, Wang et al. 2020). Except for this understudied environment, exposure to stimuli offering contradictory motion cues, was rather rare then and only concerned a proportion of the overall human population. This has significantly changed with the technological developments of the last centuries which strongly increased the exposure to passive motion cues in transportation or while using virtual displays. Most people only experience symptoms of motion sickness occasionally during their daily lives which is not surprising given that the condition is described as a “physiological response to exposure to motion stimuli that are unexpected on the basis of previous experience” (Bertolini and Straumann 2016). In line with this statement, as soon as one looks for motion sickness in more unfamiliar situations, the numbers start to grow: in an extensive questionnaire survey, Turner and Griffin (Turner 1999, Turner and Griffin 1999, Turner and Griffin 1999) asked 3256 passengers in private hire coach journeys to describe their travel experience. 22% reported to feel ‘slightly unwell,’ 4% ‘quite ill,’ 2% ‘absolutely dreadful’ and 1.7% even reported vomiting (Griffin and Newman 2004). A survey on an expedition cruise ship found that motion sickness was the most common cause of physician consultation (Schutz, Zak et al. 2014). Among

the highest incidence rates are found during spaceflight: Reschke et al. presented in their 1998 paper that 48% of cosmonauts throughout the history of the Russian space program reported space motion sickness and 60% of Skylab crew members showed symptoms (Reschke, Bloomberg et al. 1998). While (visually-induced) motion sickness is a problem nowadays already, its importance will only grow in the future, following the dawn of virtual – and augmented reality technologies for a broad audience (Keshavarz, Philipp-Muller et al. 2019, Keshavarz, Murovec et al. 2021). In addition to the traditional motion sickness experiences as described above, VR / AR and larger displays led to the introduction of a new subtype of classical motion sickness because this type of visual field stimulus is known to have a relevant nauseogenic potential (Golding and Gresty 2015). Understanding the underlying physiology is not only relevant for the development of treatment options but will also shape the economic market of the future. VR / AR will only be widely accepted by customers if they do not experience discomfort or other symptoms.

Visually-induced Motion Sickness

Visually-induced motion sickness (VIMS) can be seen as a subtype of the classical motion sickness, which shares most features and symptoms. The main difference is that VIMS is triggered by a visual stimulus in the absence of relevant physical movements (Keshavarz, Riecke et al. 2015) and “generally less severe” (Hettinger, Berbaum et al. 1990). However, intensity of the symptoms and prevalence vary widely depending on the study design, spanning a range from 1% to up to 80% of participants reporting symptoms (Keshavarz, Murovec et al. 2021). Three symptoms that are more common in VIMS compared to traditional motion sickness, are: blurred vision, disorientation and oculomotor disturbances (Lawson 2014). Depending on the exact trigger of VIMS, different names and partially dissociable, but highly overlapping concepts have been introduced: VIMS in virtual environments is often called ‘cybersickness’ (McCauley and Sharkey 1992), VIMS elicited by playing computer games ‘gaming sickness’ (Merhi, Faugloire et al. 2007), and VIMS following the usage of driving or flying simulators ‘simulator sickness’ (Hettinger, Berbaum et al. 1990). Interestingly, more modern simulators, trying to make the simulation more and more life-like, can also induce traditional motion sickness, especially when using multimodal stimulation particularly when implementing vestibular stimulation (Keshavarz, Riecke et al. 2015).

The most widely accepted theoretical framework explaining traditional motion sickness as well as VIMS, is the 'Sensory Mismatch Theory' (Reason and Brand 1975, Reason 1978, Oman 1990), suggesting that motion sickness results from a failure to integrate the (self-)motion cues from different sensory modalities (for more details see below). Other theoretical frameworks include the eye movement theory (Ebenholtz 1992) which assumes that motion sickness is closely related to asthenopia, an umbrella term for a group of somatic and perceptual symptoms related to activities commonly associated with being 'exhausting' for the eyes (Hashemi, Saatchi et al. 2019). According to this theory, the symptoms emerge due to eye movements caused by either movement in the environment or self-motion (this theory might even be traced back to (MacKenzie 1843) who described motion sickness-like symptoms following the intense usage of the eyes); this theory assumes that the combination of the optokinetic reflex, the vestibular-ocular reflex and smooth pursuit during movement in (virtual) environments, trying to avoid error-correcting eye movements, leads to muscular and nervous fatigue and asthenopia.

The postural instability theory (Riccio and Stoffregen 1991, Stoffregen and Riccio 1991) on the other hand, is based on the observation that motion sickness onset is often accompanied by increased postural instability; this framework suggests that it is indeed this increase in postural instability which causes the emergence of motion sickness (Keshavarz, Riecke et al. 2015). Bertolini and Straumann provided an excellent review and additional information on the different theories for traditional vestibular-only motion sickness (Bertolini and Straumann 2016) while works by Keshavarz and colleagues can be consulted for a comprehensive review on VIMS (Keshavarz, Riecke et al. 2015, Keshavarz, Philipp-Muller et al. 2019, Keshavarz, Murovec et al. 2021). Because sensory mismatches and the visuo-vestibular conflict are recurrent topics, the following paragraph will go into this a bit more.

Sensory Mismatch Theory

The basic idea is that motion sickness is caused by conflicts between input from different motion-sensitive sensory modalities (mainly from the visual, the vestibular and the somatosensory system (Reason and Brand 1975), but theoretically possible also from the auditory and potentially olfactory system, albeit the latter probably not in humans) and expectations or efference copies (Bertolini and Straumann 2016). A good example

is the exposure to optic flow during a virtual rollercoaster task: the visual input is interpreted as forward self-motion while the vestibular system signals stationarity. This setting would typically lead to vection experience but is not automatically sufficient to cause motion sickness. Motion sickness, according to the theory, will be experienced if there is a deviance between expected and experienced sensory input or a conflict between the signals from different sensory modalities respectively. And indeed, adaptation seems to be the most effective (long term) treatment approach (Golding and Gresty 2015). In the light of the Sensory Mismatch Theory, adaptation can be interpreted as the process of updating the expectations to the actual experience or learning that the sensory input from two modalities can be incongruent. This could explain why patients with compensated bilateral labyrinthine deficits, and therefore without vestibular input, had no unexpected visuo-vestibular conflicts and subsequently experienced no motion sickness at all while healthy controls reported symptoms in 21 of 27 trials (Cheung, Howard et al. 1991). For a more in-depth discussion of clinical aspects see the general discussion and the chapter on ‘Clinical relevance’.

1.8 Aims of the studies and hypotheses

The main aim of our studies was to develop optic flow stimuli which reliably induce a sufficient degree of vection while at the same time being short enough to allow for a time-locked analysis of postural and neurophysiological responses with an adequate number of trials per participant. This was the basis for addressing the question whether self-initiation of otherwise identical optic flow stimuli leads to differences in the processing and perception of those stimuli. In line with the sensory attenuation observed in other sensory modalities, we expected to observe either lower amplitudes of the ERP or a modulation of early components and weaker ERD in the self-initiated compared to the passive flow conditions. On the behavioural level, we expected the participants to rate their vection experience as well as their VIMS intensity lower in the self-initiated conditions. On the postural level, we anticipated the postural responses to be more time-locked in the self-initiated flow condition and expected either a stronger amplitude because of anticipatory movements in the active condition as shown in prior studies on virtual driving (Dong, Yoshida et al. 2011) or a lower amplitude of the postural responses in self-initiated trials due to either self-specific or

general predictive mechanisms in line with sensory attenuation. Additionally, we addressed the question whether a chin-rest is effectively able to inhibit head movements as is generally assumed. In addition to that, we predicted that mobile EEG is able to reliably identify the most important ERP components and show a modulation as long as the effect is sufficiently strong.

2. Methods

To address and connect the different topics presented in the introduction, this thesis consists of three similar but distinct experiments all addressing the relationship between optic flow, vection and active control over the stimuli in slightly different ways. The experiments look at different postures (standing in Experiment 1 and 2 and sitting in Experiment 3), different types of optic flow (continuously expanding/contracting in Experiment 1 and a combination of accelerating and continuous expanding patterns in Experiment 2 and 3), are purely behavioural (Experiment 1) or also include measurements of postural sway and EEG (Experiment 2 and 3) and include speed estimations (Experiment 2) and VIMS ratings (Experiment 3). The common features of the three experiments are described below.

	Experiment 1	**Experiment 2**	**Experiment 3**
posture:	standing	standing	sitting
practice trials:	✗	✓	✓
optic flow direction:	expanding or contracting	expanding	expanding
optic flow profile:	continuous	acceleration + continuous	acceleration + continuous
button-press-control	✗	✗	✓
chin-rest	✗	✗	✓
optic flow offset:	sudden offset	sudden offset	static frame
optic flow duration:	5 s	2 s	2 s
EEG:	✗	✓	✓
accelerometer:	✗	✓	✓
VIMS rating:	✗	✗	✓
vection rating:	✓	✓	✓
speed rating:	✗	✓	✗
VAS orientation:	horizontal	horizontal	vertical

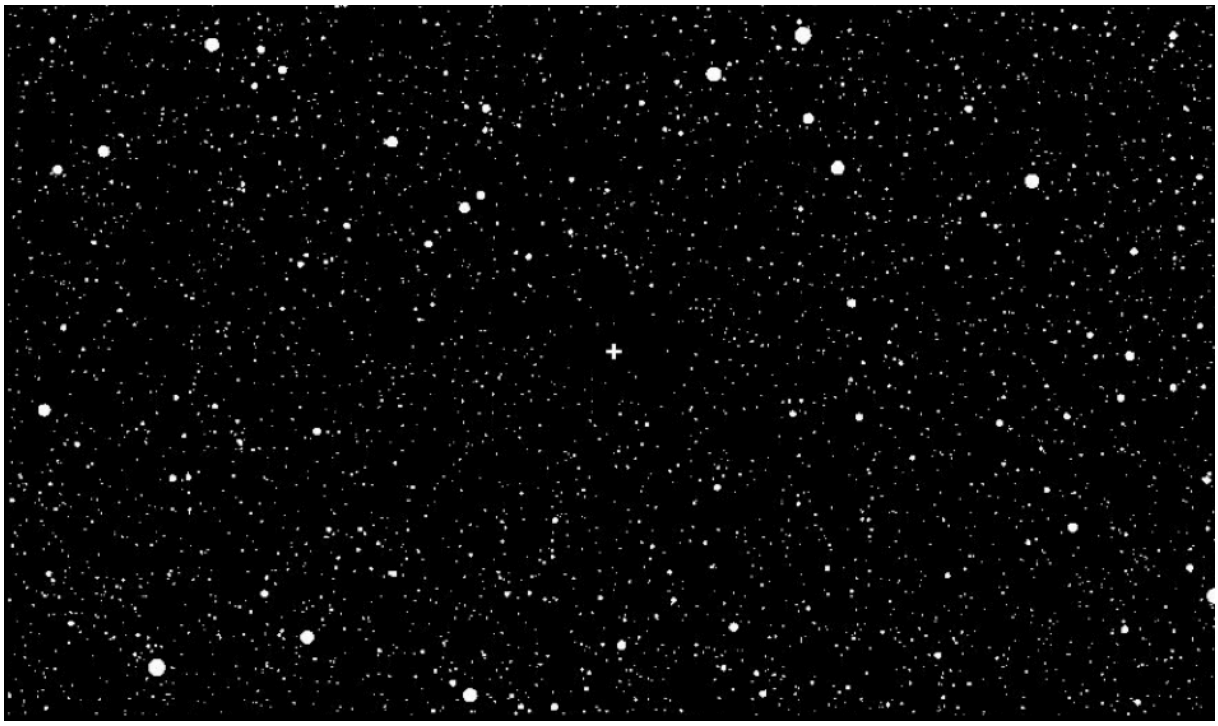

Figure 1: the static frame consisting of the white fixation cross in the centre of the field of view and the dots in various sizes and apparent depths.

2.1 General Procedure

Each participant was evaluated whether they fit to the inclusion criteria: 1) age between 18 to 36; 2) no history of neurological, psychiatric or vestibular disorders and 3) normal or corrected to normal vision; handedness was assessed by a version of the Edinburgh Handedness Inventory (www.brainmapping.org, adapted from (Oldfield 1971), last access: 12.12.2022). Only participants with a laterality index ≥ 50.00 on the standard inventory were accepted. Participants received an information sheet (see appendix) in Experiment 2 and 3 to make sure that everyone gets the same instructions including a written definition of vection. In Experiment 1, the instruction was verbally and semi-structured. Afterwards, they signed the consent form, and the EEG was set up. Two different cap sizes were used dependent on the participant's head diameter. The electrodes were placed according to the 10-10-system only using channels O1, O2, P3, P4, P7 and P8. The signal was referenced to A2 and re-referenced offline to A1. The ground electrode was positioned on Fz. To allow the removal of blink artifacts, we placed one electrode below the right eye (vertical EOG). In a pocket at the back of the caps, we placed the amplifier with the built-in accelerometer, measuring head- and body acceleration along three orthogonal axes in [mg] ($= 9.81 * 10^{-3}\ \frac{m}{s^2}$). Data was

recorded with the Brain Vision Recorder software using the LiveAmp amplifier from Brain Products (Gilching, Germany). Impendence for all channels was kept ≤ 10 kW and sampling rate was set at 1000 Hz. The height of the projector was adjusted by moving the fixation cross with the whole display to the centre of the participants' field of view. Participants wore custom-made glasses which reduced their field of view to approximately 90 x 60 degrees of visual angle to prevent that they could see the edges of the screen, to block out diffuse light from the recording computer monitor and focus their attention on the screen. Each experiment followed the same overall procedure with randomized order of agency blocks. First, they performed 5 active and 5 passive practice trials. After practice completion, participants were asked whether they have any questions. If everything was clear, the main experiment began. It consisted of a variable number of trials dependent on the experiment. Participants were instructed to take breaks between two blocks. Each trial followed the same scheme: the static frame (Figure 1) was presented either for a random time between 1 and 2 seconds in the passive condition or until participants decided to press either the forward or backward arrow (Experiment 1) or the left mouse button with their right index finger (Experiment 2 and 3) to start the optic flow in the active condition. After each trial, participants were asked to rate their subjective experience (speed relative to reference speeds and/or vection) of the optic flow on a visual analogue scale (VAS). Participants rated by moving the cursor along the scale (Figures 11, 19 and in the task figure in the publication) and pressing the left mouse key at the position which fit their experience. The coordinates of the button press were used to calculate the response which was a rational number between 0 and 100. Ratings below 0 or above 100 were registered as 0 and 100 respectively.

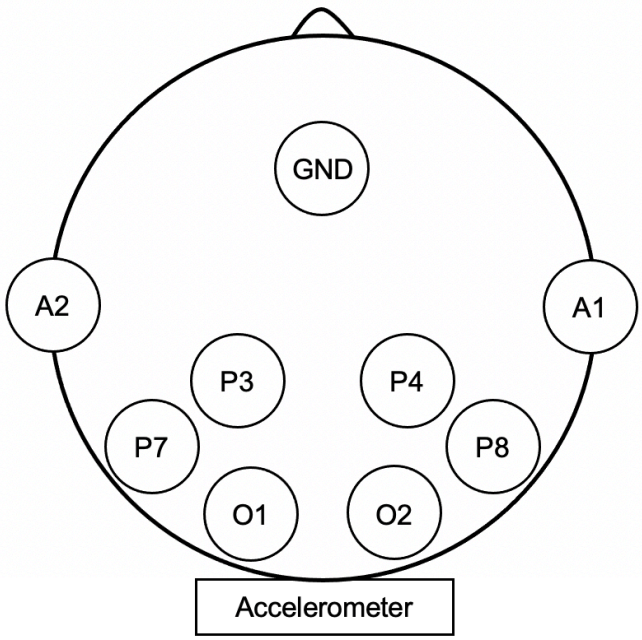

Figure 2: Montage of the EEG electrodes and the accelerometer. Modified from (Obereisenbuchner, Dowsett et al. 2021)

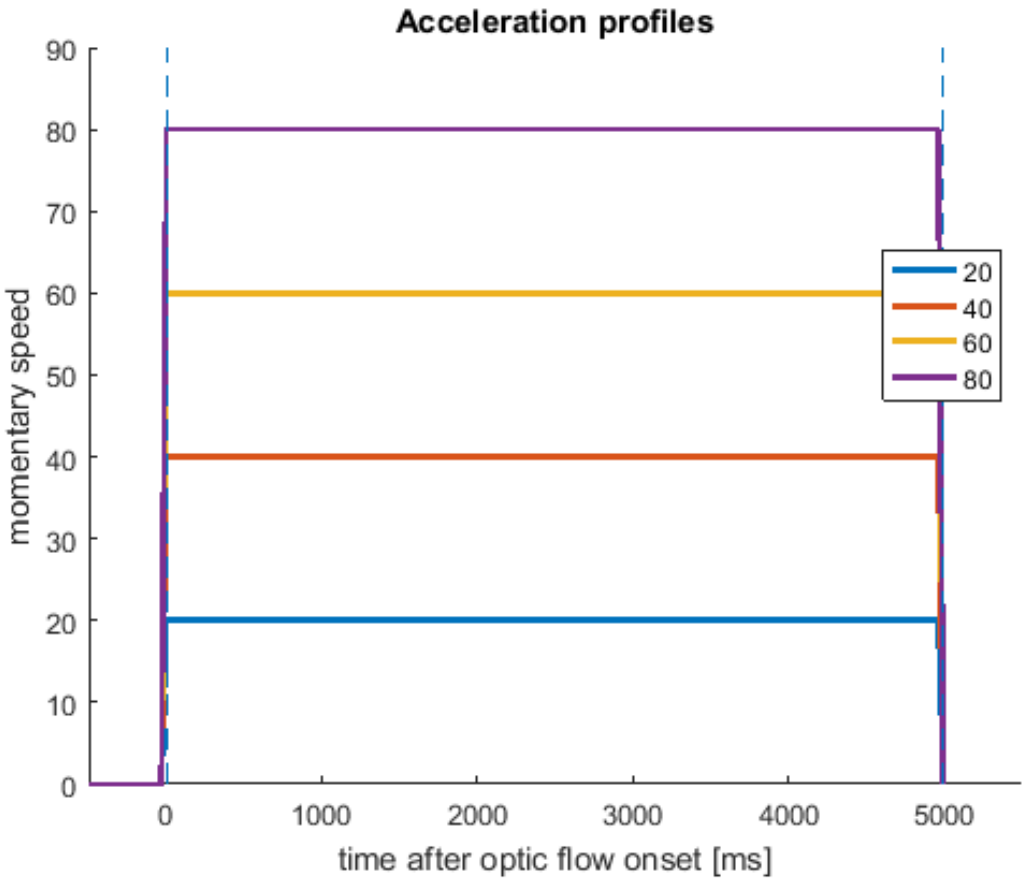

Figure 3: The different acceleration profiles used in Experiment 1. Participants were shown radially-expanding or -contracting optic flow displays with four different constant velocities for 5 seconds which started right away and ended without the presentation of a static frame before the VAS appeared.

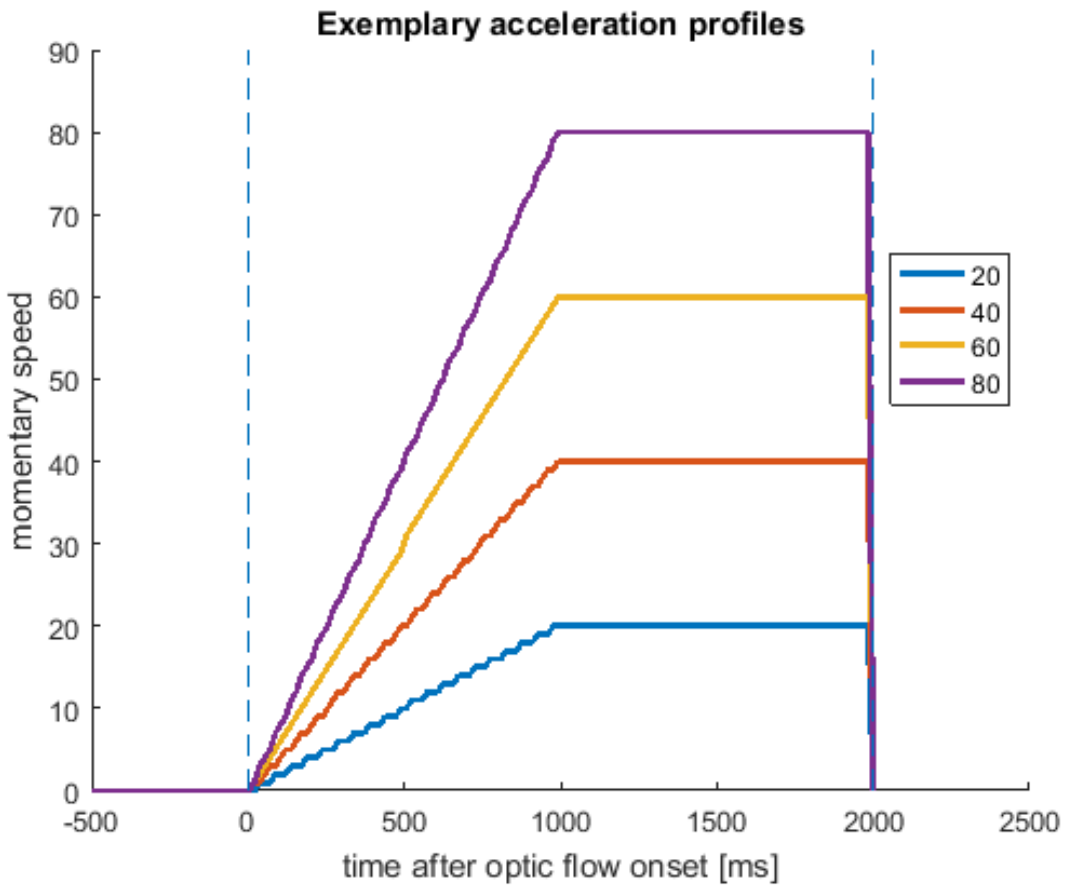

Figure 4: Four (out of 80) different example acceleration profiles used in Experiment 2. Participants were shown radially-expanding optic flow displays with four different peak velocities for 2 seconds which started with a 1 second acceleration phase followed by 1 second of continuous optic flow. The stimuli ended without the presentation of a static frame before the VAS appeared.

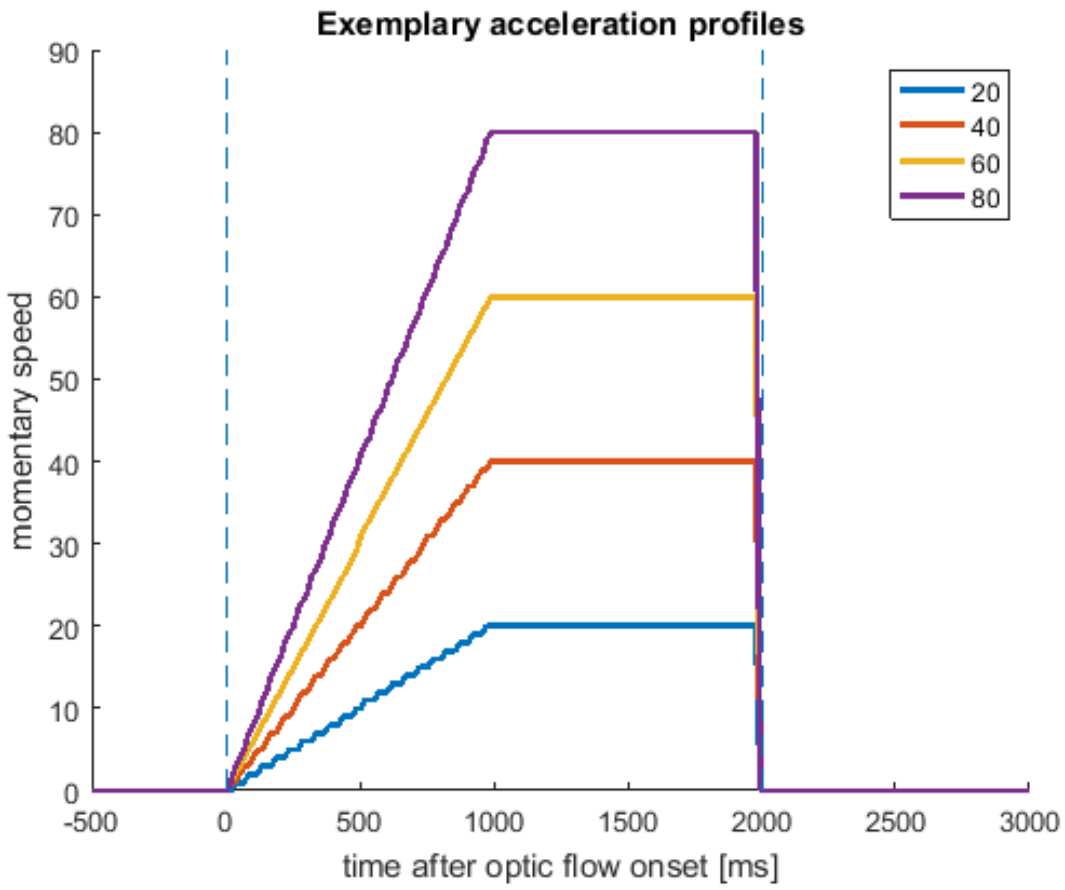

Figure 5: Four (out of 80) different example acceleration profiles used in Experiment 3. Participants were shown radially-expanding optic flow displays with four different peak velocities for 2 seconds which started with a 1 second acceleration phase followed by 1 second of continuous optic flow. After stimulus offset, a static frame was shown for 1 additional second before the VAS appeared.

2.2 Accelerometer

The built-in accelerometer as part of the LiveAmp from Brain Products was put in a pocket (which was part of the two different size mobile-EEG caps) at the back of the participant's head and fixated using the strap of the custom made googles to avoid any artificial oscillations other than head-/body sway. It recorded acceleration in all three spatial directions orthogonal to each other (see Figure 6). The sampling rate was also set to 1000 Hz and the data were transferred wirelessly to the data collection PC using the Brain Vision Recorder software. The three accelerometer directions were treated as separate channels and therefore the EEGLAB-based data extraction and filtering techniques applied for the EEG channels could be applied on the accelerometer data simultaneously.

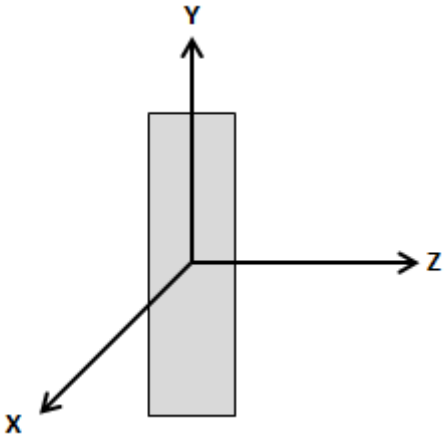

Figure 6: The outline of the accelerometer (light grey) and the three recorded, orthogonal dimensions in the upright position of the participant. Positive acceleration was registered whenever the participant moved in the direction of the arrows. 'x' corresponds to medial-lateral, 'y' to up-down, and 'z' to anterior-posterior. The axes are referenced relative to the accelerometer not to the gravitational vector.

Accelerometer Tilt

The resulting coordinate-system needed to be referenced to a common scheme as the accelerometer was variably tilted around the x-axis because of anatomical differences of the occipital bone and design differences between the small and large cap. The main problem of this is that the same backward acceleration will produce a signal which consists of a weighted Y and Z component, both depending on how strong the tilt was. This can be explained best with the registration of the gravitational vector in a static, upright accelerometer as shown in Figure 6: if the accelerometer was not tilted at all, then X and Z should show zero while Y shows |g|. But if the accelerometer is rotated around the x-axis by say 20°, then X would still signal zero, while Y and Z show non-zero values as the magnitude of g is split up on those two channels in a non-linear way. But this problem can easily be circumnavigated by using an approach based on fundamental trigonometry: First, assuming that people held their head upright and statically aligned to the gravitational vector during the baseline periods, it is possible to determine the individual accelerometer tilt by calculating the arctan of the mean of all the Z signals during baseline divided by the mean of all the Y signals during baseline:

$$tilt\ [°] = \tan^{-1}\left(\frac{baseline_Z}{baseline_Y}\right)$$

To be able to better understand why this is true, it is helpful to look at the relationships on a unit-circle with r = |g|:

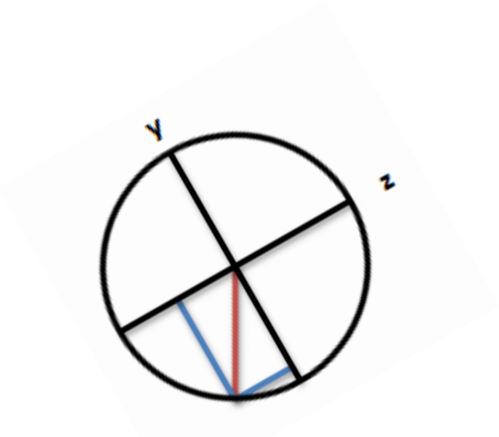

Figure 7: 2D-projection of the tilted accelerometer axes normalized by the magnitude of the gravitational vector (red) shows how the measured Y and Z signals always add up to the magnitude of the gravitational vector and the relationships between the different angles.

Figure 7 shows that the accelerometer tilt angle is identical with the angle between the gravitational vector and the y-axis of the accelerometer, which again is identical with the angle between gravitational vector and the measured Y signal. This allows to calculate the angle via the trigonometric approach.

Virtual Channel

Identifying a way to determine the individual tilt is only the first step. To allow inter-participant comparison of the postural sway, it is crucial to find a weighted way of adding the Y and Z component of the signal to obtain the real translational acceleration. An easy and efficient way of doing this was to analyse the magnitude of the forward - / backward acceleration vector in form of a virtual channel in the following way:

$$|v(t)| = \sqrt{y(t)^2 + z(t)^2}$$

v =: the reconstructed anterior-posterior acceleration
y =: the acceleration recorded along the y-axis of the accelerometer
z =: the acceleration recorded along the z-axis of the accelerometer
t =: the time after optic flow onset

The advantage of this method is that the magnitude is independent of the tilt in the relevant tilt-window of 0 - 75° (see Figure 8). However, this approach has an inherent limitation: the information about direction of acceleration is lost because of the square of the raw values. To overcome this problem, it is possible to normalize the raw Z

values and multiply the resulting array with the magnitude of the virtual channel. In the relevant tilt-window of a clockwise rotation of <75°, this normalized array will always contain +1 for backward - and –1 for forward acceleration. Using this approach, the direction information can be reconstructed in the virtual channel for each data point.

$$\|z(t)\| = \frac{z(t)}{|z(t)|}$$

$$v(t) = |v(t)| * \|z(t)\|$$

To test whether this approach works, we designed a short experiment which included 10 standardized accelerometer backward movements with different tilt angles. One can assume that the method works if the plots (Figure 8) with the different tilt angles show essentially the same amplitude and overall pattern.

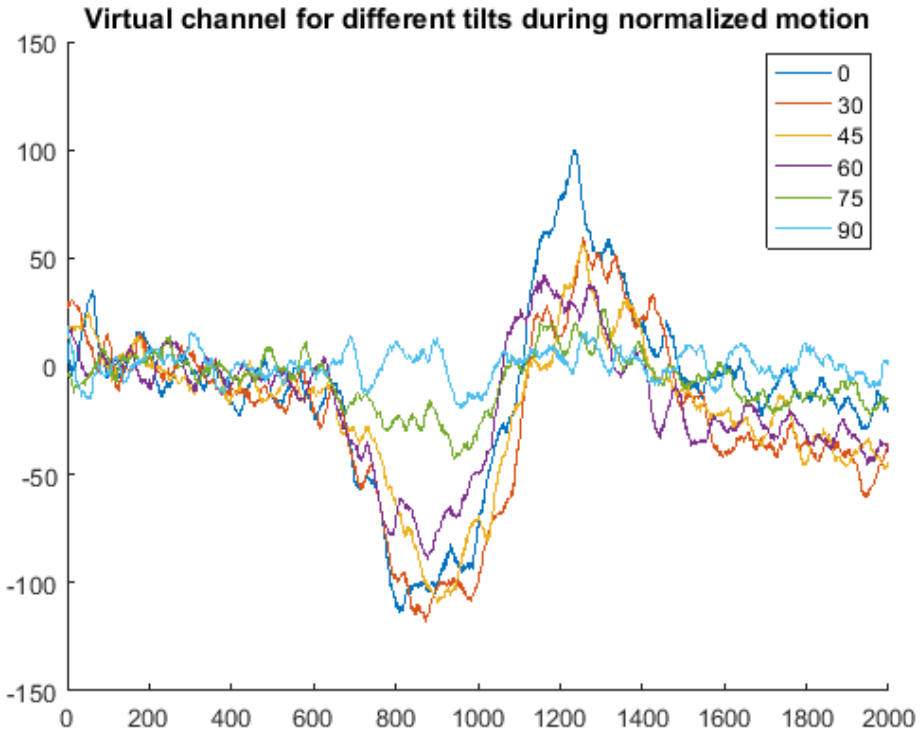

Figure 8:. The different plots show the acceleration after reconstruction via a virtual channel for different tilts of the accelerometer. The curves for 0° - 45° are almost identical as they ideally should be and the curve for 60° only mildly deviates.

And indeed, Figure 8 shows that the approach seems to work for the relevant tilts of 0° - 45° which were seen during the analysis of the experimental data. Therefore, we decided to use this approach for all types of accelerometer analyses.

2.3 Electroencephalography

Electroencephalography (EEG) is a non-invasive method of measuring differences in electrical potentials of large groups of mainly cortical neurons with very high temporal resolution, making it a useful technique to study the dynamics of the brain and their relation to cognition and disease (Cohen 2017).

History

Richard Caton presented his ground-breaking findings that it is possible to register electrical currents from the brains of living monkeys and rabbits using a galvanometer, at the Annual Meeting of the British Medical Association in 1875 (Caton 1970). Around 1890, Beck was able to localize brain regions where the electrical currents can be modified by stimulation of different peripheral sensory organs (Berger 1929). In 1912, Kaufmann demonstrated that there are spontaneous changes in electrical currents throughout the cerebral cortex (Kaufmann 1912). Wladimir Práwdicz-Neminski dissociated two types of cortical oscillations: waves of the first (10-15 Hz) and second order (20-32 Hz) (Práwdicz-Neminski 1925). Hans Berger, the physician who is well known for being the first to measure the "Elektrenkephalogramm" in humans, further distinguished two types of brain activity: the spontaneous, ever present current and changes in this current in response to stimulation of peripheral sensory organs. His first experiments were performed in humans with pre-existing openings in the skull, mostly due to craniotomies performed in order to relieve intracranial pressure, allowing epidural recordings; later he moved on to use superficial electrodes over bone defects and finally, he was able to measure the current non-invasive in healthy subjects (Berger 1929). Interestingly, already in 1929, Berger was convinced that the first and second order waves reflect ongoing cortical activity, and that the cortex is active even if the person is asleep or anesthetized.

Physiological Basis

Even though there have been discussions on the underlying neurobiological and neurophysiological correlates for the EEG signal almost since the beginning of EEG, there are some aspects which are widely accepted within the scientific community. Namely that the EEG signal seems to be caused by the synchronous firing of large clusters of cortical neurons, especially from superficial layers (Cohen 2017). Simulations by Murakami and Okada estimated that at least about 10000 – 50000 cortical pyramidal neurons firing in synchrony are needed to register a signal with EEG (Murakami and Okada

2006). But what exactly does the EEG measure? It is commonly assumed that discharging neurons produce a dipole between the intra- and extracellular space, e.g. the (dendritic) postsynaptic potential which probably is the most important contributor to the local field potential (Lopes da Silva 2013). Therefore, the extracellular fields of clusters of neurons firing in phase with similar geometric orientation superimpose and the resulting field is measured with the EEG (Nunez and Srinivasan 2006). But as Buzsáki et al. point out, "any type of transmembrane current contributes to the extracellular field", for example the prominent and probably most important synaptic activity, but also long-lasting Ca^{2+}-spikes, after-hyperpolarization and even gap junctions and neuron-glia interaction (Buzsáki, Anastassiou et al. 2012). So, the dipole explanation is good, but not sufficient to fully understand EEG. Mike X. Cohen summarized the situation quite well: "…[T]he relationship between EEG and LFP depends on several factors that are imperfectly understood" (Cohen 2017). While this leads to a gap in our understanding of how the different scales in the neuronal system interact, Nunez and Srinivasan pointed out that higher-order functions can be better observed using large-scale methodology while they correlate poorly with single-cell recordings (Nunez and Srinivasan 2006).

Data analysis

During each participant's experiment, we recorded the EEG and accelerometer data with a resolution of 1000 Hz which was stored in the form of a header and a binary data file, containing the channels' voltage values and the acceleration data. In addition, we obtained a marker file with the triggers that were sent during the start of optic flow. The behavioural responses as well as the type of trial ("self-initiated" or "passive flow") and the speed of the optic flow were stored in a spreadsheet. In the next step, the data was extracted using EEGLAB (v13.5.4b) to create a matrix containing the six EEG channels, the second reference to the left ear, the EOG, the three-dimensional accelerometer data, and the virtual anterior-posterior channel computed as described above. The EEG and EOG data was re-referenced to the signal from both ears and subsequently low- (<40 Hz) and high-pass filtered (>0.3 Hz) following the settings from Probst et al. (Probst, Plendl et al. 1993) using *filtfilt()*. The accelerometer data was filtered using the same settings based on the absence of information in literature and visual inspection of the resulting curves. The virtual channel was computed using the raw data and filtered afterwards. The resulting matrix was then stored for each individual participant to save computation time in the later steps of the analysis.

The ERPs / VIPRs were epoched to the onset of optic flow by using the triggers in the marker file. The preceding 200 ms / 500-301 ms were used for baseline correction by subtracting the mean of the voltage / acceleration during baseline from each data point during the 500 ms or 1000 ms trial period, as suggested by Cohen (Cohen 2014). EEG trials were rejected where the signal range of the EOG during the trial or baseline period exceeded 100 mV (corresponding to e.g. a blink, based on visual inspection of the raw data) or the signal range in any one channel exceeded 120 mV (corresponding to e.g. a movement artifact or loose channel, based on visual inspection of the raw data). Accelerometer trials were excluded if the baseline was skewed as indicated by a signal range exceeding 40 mg or a peak amplitude during the trial exceeding 50 mg (corresponding to non-optic flow related movement artifacts, as based on visual inspection of the raw data). The ERPs / VIPRs were computed by calculating the grand average (taking the mean of the individual participant's mean of all individual trials within the respective conditions). The time-frequency analysis was done using complex Morlet wavelet convolution based on the fast Fourier transformation as described by Cohen, including suggestions for parameters and information on how to avoid artifacts (Cohen 2014). Our parameters were set to a frequency window of 4 - 20 Hz with individual frequencies being calculated using a logarithmically spaced approach with the respective frequencies as the boundaries (Cohen 2014). To avoid edge artifacts, we used longer epochs from 3.5 s before to 3.5 s after optic flow onset while only displaying the interval from -200 ms before to 2 seconds after optic flow onset (the trial removal described above for ERPs was prolonged accordingly). In the figures, the data is presented after decibel conversion to show the change in magnitude of the frequency-band specific activity compared to pre-trial baseline.

The decision between parametric (t-test) and non-parametric tests (Wilcoxon Signed Rank) was based on automatized testing for normality and equality of variances by using *lilietest()* and *vartestn()*. Wherever multiple channels were tested, Bonferroni-correction was applied.

3. Experiment 1

Behavioural Effects of Expectancy and Control on Vection Experience: an exploratory study.

3.1 Introduction

The aim of this first exploratory study was to use the either radially-expanding or contracting optic flow stimuli that were already known to reliably induce linear vection in other experiments done in our lab (e.g. (Dowsett, McAssey et al. 2017) and unpublished pilot studies) and see whether different levels of control over the stimuli lead to a modulation of vection perception. Another goal was to dissociate different levels of control; namely to see whether participants experience a situation in which they are instructed to press a certain button and can only choose when they want to press it, as a situation in which they experience comparable agency to a situation in which they can also choose the button and therefore the direction of optic flow. This question is important given e.g. the conceptual and methodological criticism of the famous Libet Experiment (Libet, Wright et al. 1982, Libet, Gleason et al. 1983) by Kihlstrom and Papanicolaou (Kihlstrom 2017, Papanicolaou 2017) and the fact that various studies on sensory attenuation assume that instructed self-initiation of stimuli in the absence of free or forced choice is effectively modulating agency, e.g. Baess et al. and Weiss et al. (Baess, Horváth et al. 2011, Weiss, Herwig et al. 2011)).

We expected that participants report the experience of both forward and backward vection in the respective conditions. We predicted that agency is rated higher in both the choice and the forward - / backward-instructed conditions compared to the passive condition.

Based on the sensory attenuation literature (see Chapter 1), one would expect vection to be rated lower in the higher agency conditions. However, this might be due to the more complex nature, the multiple cognitive influences, the high inter-individual variability of vection compared to traditional stimuli used in the sensory attenuation literature, and the fact that it has not been possible to show meaningful modulation of the vection experience with active control in earlier studies (Riecke and Feuereissen 2012). We therefore assumed that sensory attenuation of vection experience while logically quite possible, will probably not be observable on a behavioural level, at least not on the group level.

3.2 Methods

Participants

10 healthy, young (mean age ± SD: 23.5 ± 7.3, range: 20 - 43; 5 females; 8 right-handed, 2 left-handed) adults with no history of neurological or psychiatric disorders and normal or corrected to normal vision participated in our study. All subjects provided written and informed consent and were financially compensated for their participation.

Procedure

Each participant was evaluated as to whether they fitted the inclusion criteria: no history of neurological, psychiatric, or vestibular disorders and normal or corrected to normal vision; handedness was assessed verbally during the briefing. Because of the purely exploratory role of this study, left- and right-handed participants were included. Participants were verbally instructed and vection was explained to them as the subjective feeling of ego-motion (importantly, we did not use the same written formal definition as was developed for Experiment 2 and onwards). The experimenter tried to give the same standardized information to each participant. After the instructions, they signed the consent form and were shown the exact standing position in front of the screen as well as the handling of mouse and keyboard which were placed on separate high-adjustable tables to their right (mouse) and left (keyboard). The height of the projection was adjusted by moving the fixation cross with the whole display to the centre of their field of view (see Figures 10 and 11). Participants were instructed to stand in a comfortable upright position. Dependent on either chosen direction (choice condition), instructed direction (forward- and backward instructed condition), or randomly selected direction (passive), participants were exposed to 5 seconds of either radially expanding or contracting optic flow with different constant velocities. Figure 9 shows the different conditions which were presented in randomized order within each of the nine experimental blocks.

speed	choice	forward instructed	backward instructed	passive	total
20	2	1	1	2	6
40	2	1	1	2	6
60	2	1	1	2	6
80	2	1	1	2	6
total	8	4	4	8	24

Figure 9: Overview of the number of trials per agency condition, optic flow speed, and direction of simulated self-motion within each of the experimental blocks. Note that the direction in the choice condition was selected by the subject and that the direction in the passive condition was randomly selected with forward and backward being equally probable.

Each trial (see Figure 11 for an overview) started with a static frame, followed by a colour change of the fixation cross. Grey indicated a 'passive trial', with a random direction of the optic flow approximately 500 ms after the end of the cue. In 'instructed trials', participants had to press either the up-arrow on the keyboard with their left index finger to start radially expanding (=forward) optic flow (green cue) or the down-arrow with their left thumb to start contracting (=backward) optic flow (blue cue). Finally, in 'choice trials' (red cue) they could freely decide which direction they prefer. Within each block, each of those conditions was combined with all of the four different speeds. Important here is that the optic flow was presented at a continuous velocity, without following the aforementioned acceleration profiles as used in the other experiments. Instead, it reached the maximum speed right away, went on for 5 s with constant velocity followed directly by the horizontal visual analogue scale for the vection judgements.

Each participant was presented with 72 choice, 36 forward-instructed, 36 backward-instructed, 36 forward-passive and 36 backward-passive trials (total of 216 trials).

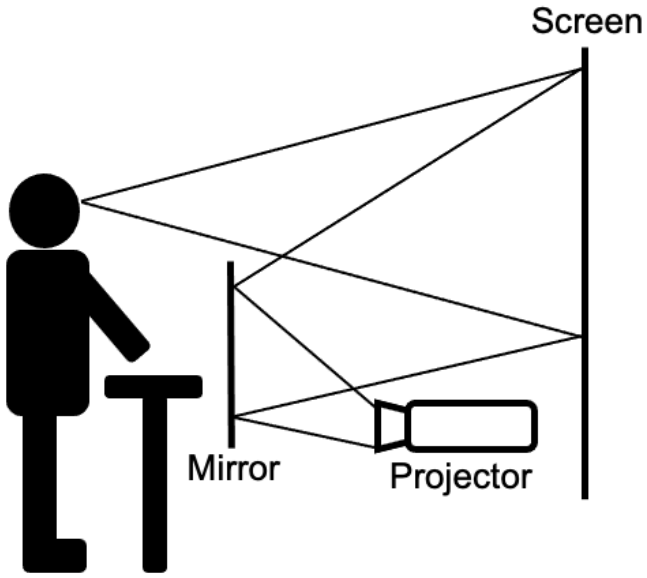

Figure 10: Setup of the projector and participants' posture relative to the screen. The eye-screen distance was 1.15 m and the visual angle 90° x 60°. The mouse (right hand) and keyboard (left hand) were placed on the table in front of the participants.

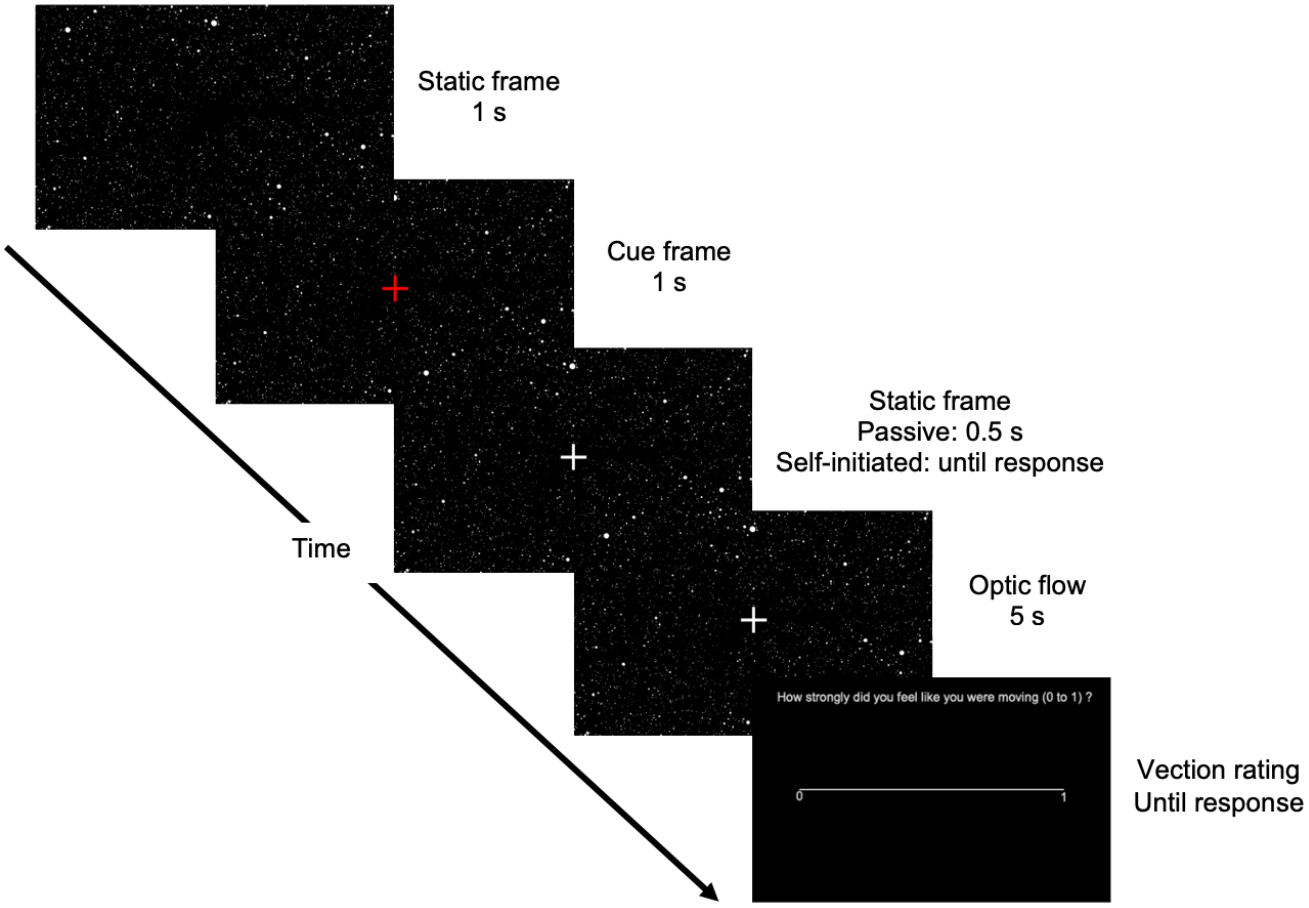

Figure 11: Task schematic visualizing the different agency conditions. On self-initiated flow trials (choice, forward- and backward-instructed) participants initiated the flow onset by pressing a button. On passive flow, the flow was started by the computer and they did not press a button. The presented optic flow was either radially expanding or contracting.

3.3 Results

Vection results

The mean vection rating was 52.5 ± 4.3 out of 100 on the VAS. A one-way ANOVA was performed to compare the effect of agency condition on vection experience, indirectly measured via subjective VAS ratings. A one-way ANOVA revealed that there was no statistically significant difference between either two groups F(3,36) = 0.2134, p = .8865. Tukey's HSD Test for multiple comparisons was therefore not done.

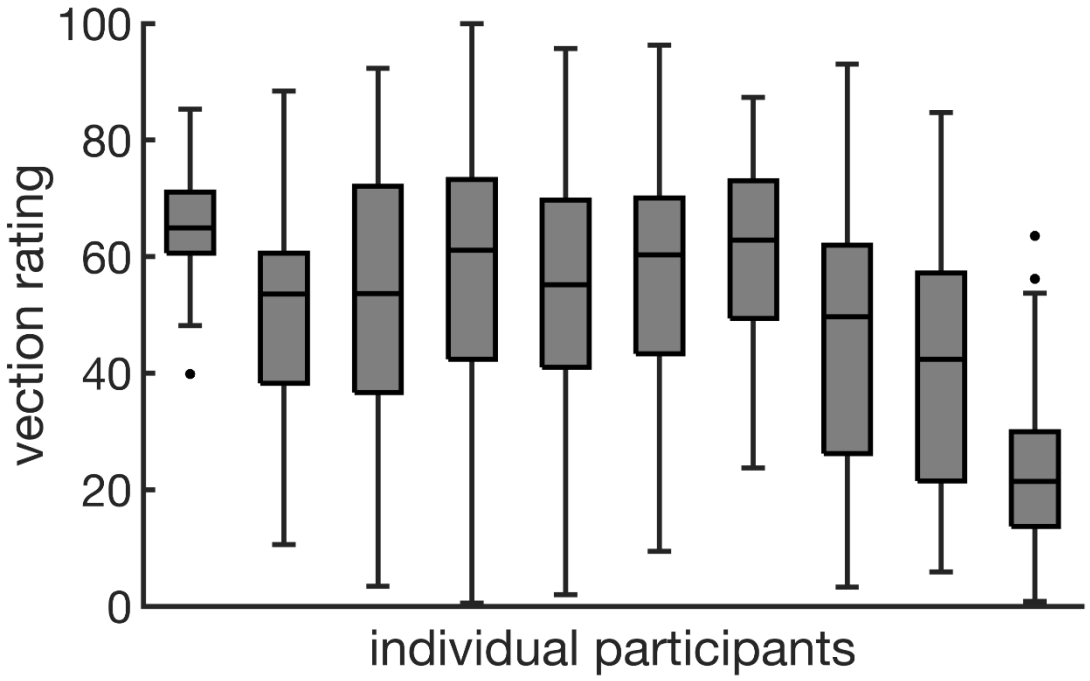

Figure 12: Individual vection ratings and variability over the course of the experiment. Horizontal lines inside the boxes correspond to the median of vection ratings. The boxes show interquartile range. The whiskers show the highest and lowest non-outlier rating (quartiles defined as 0.75 respective 0.25 quartiles).

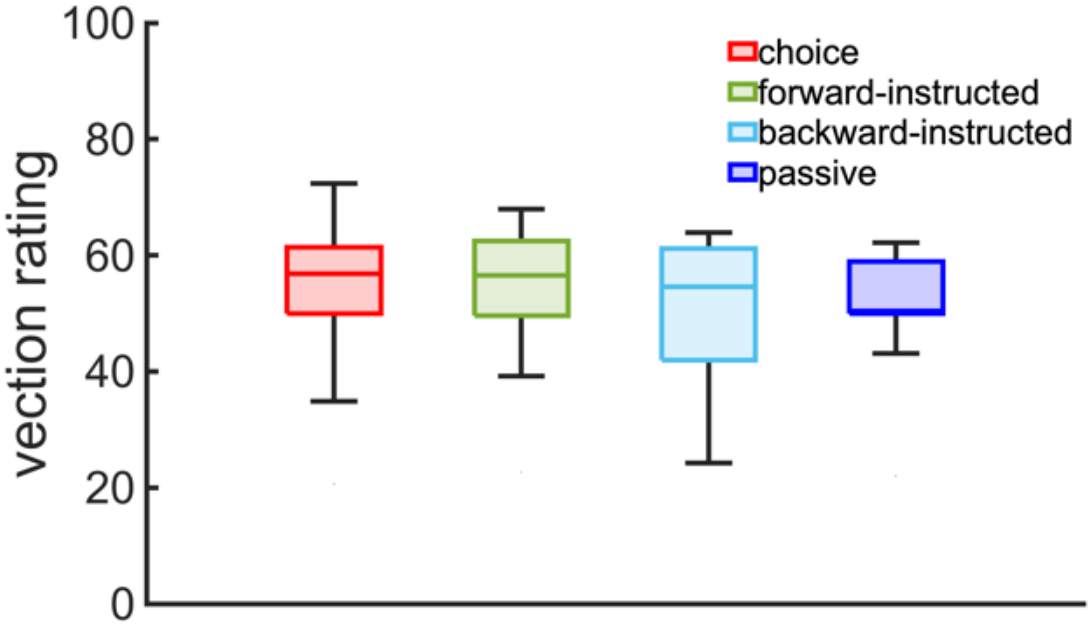

Figure 13: Comparison of the vection ratings in choice (red), forward-instructed (green), backward-instructed (light blue) and passive trials (dark blue). The horizontal line in the box plot shows the median, the box marks the inter-quartile range, and the whiskers show the highest and lowest non-outlier values. The vection ratings did not differ between agency conditions.

Agency results

We analysed whether participants rated their perceived level of control over stimulus motion onset differently in the various agency conditions (Figure 14). A one-way ANOVA was performed to compare the effects of agency condition on agency rating. There was a statistically significant difference in agency ratings between either two groups $F(3,36) = 6.9463$, $p = .0008$. Tukey's HSD Test for multiple comparisons found that the mean value of agency ratings was significantly different between "choice" and "passive" ($p = .0004$, 95% C.I. = [21.1389, 83.2039]) as well as between "forward-instructed" and "passive" ($p = .0439$, 95% C.I. = [0.6532, 62.7182]). There was no statistically significant difference between "choice" and "forward-instructed" ($p = .3003$), "choice" and "backward-instructed" ($p = .1357$) "forward-instructed" and "backward-instructed" ($p = .9697$), "backward-instructed" and "passive" ($p = .1164$). Figure 15 shows the ratings the individual participants gave and connects each participant with a line; notice that there seems to be a dissociable rating strategy: while most participants experience almost the same agency in choice and the two instructed conditions, two

subjects rate their agency with almost zero in the instructed conditions. This is interesting, given the fact that they themselves initiated the optic flow with a button-press. Another interesting finding is that participants surprisingly preferred the radially-expanding optic flow in forward-instructed; out of the 72 choice trials, they have chosen forward significantly more often (52.0 ± 3.0 times) and (backward 20.0 ± 3.0 times) as shown by a paired-sample two-tailed t-test ($t_9 = 5.54$, $p \leq .001$).

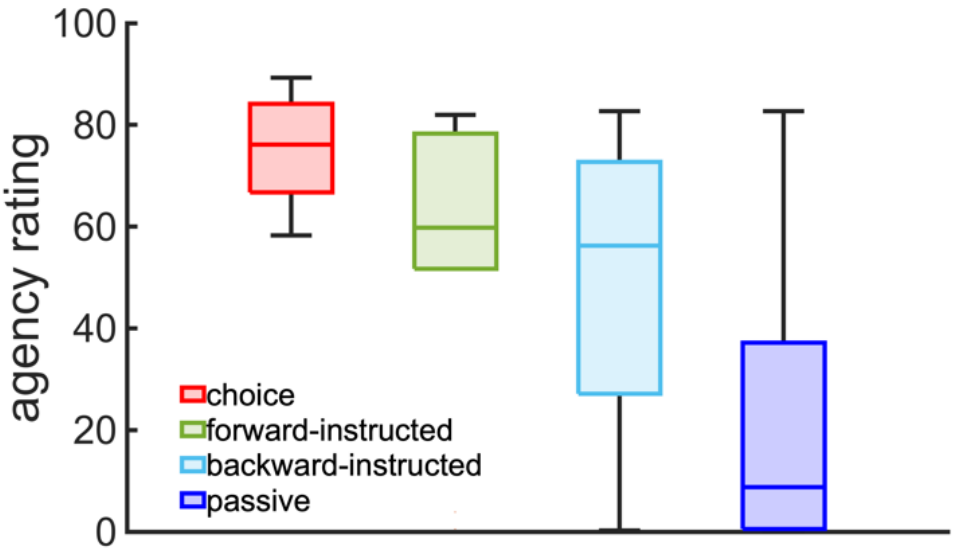

Figure 14: Comparison of the ratings of the experienced level of control in choice (red), forward-instructed (green), backward-instructed (light blue) and passive trials (dark blue). The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. The agency ratings in backward instructed and passive trials showed high inter-individual variability and agency was effectively modulated by the different agency conditions.

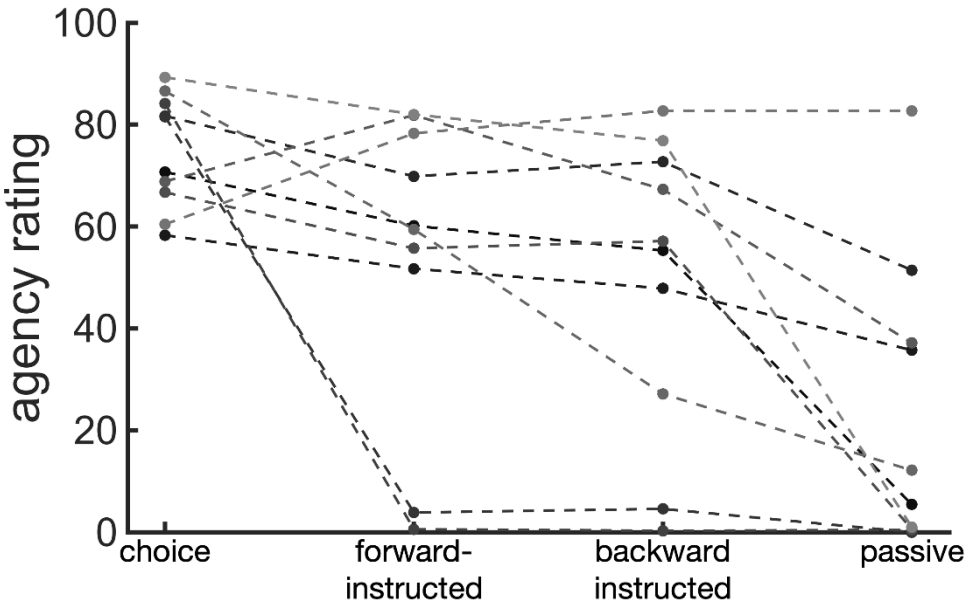

Figure 15: Comparison of the ratings of the experienced level of control for individual participants. Each participant's ratings are connected by dashed lines. The agency ratings in backward instructed and passive trials showed high inter-individual variability and agency was effectively modulated by the different agency conditions. Two participants seem to have not experienced the instructed condition as if they were in control of stimulus onset (almost zero ratings in forward- and backward-instructed).

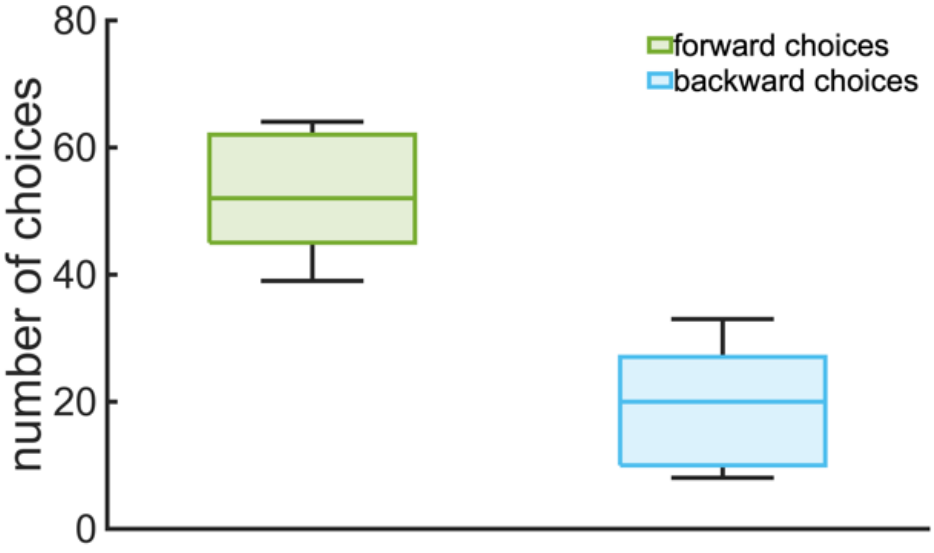

Figure 16: Comparison of the number of forward (green) and backward choices (blue) when participants were able to choose the direction. The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. The figure shows a clear preference of forward motion simulating optic flow.

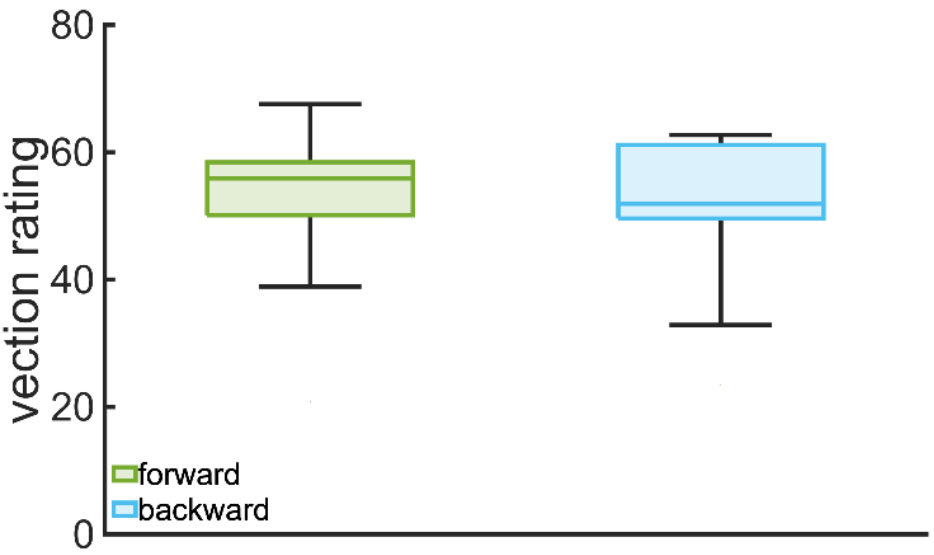

Figure 17: Comparison of the rating of the vection experience in trials simulating forward (green) and backward translation (blue). The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. The vection ratings did not differ between conditions.

3.4 Discussion

In general, our predictions were meet. In line with the literature, we found that there was a high positive association of optic flow speed and vection ratings for most participants (Tamada and Seno 2015). Informal debriefing after the experiment points in the direction that participants experienced vection based on their verbal description.

Agency and levels of choice

Participants consistently reported higher agency in the choice condition with two degrees of freedom (direction, timing) and in the forward-instructed condition with one degree of freedom (timing) compared to the passive condition. While this result is not surprising, it is nonetheless an important basis for future experiments as it backs up the claim that control over the onset timing is enough to give participants a significantly different agency experience and self-initiation without direction choice will be sufficient to address our research question. It is however important to note that participants' assessment of their control in the instructed conditions differed: there were two participants who showed a distinct pattern (see Figure 15); maybe they applied a more abstract and less mechanical conception: while they ultimately pressed the button themselves, they did not form the intention intrinsically. This has important implications for e.g. moral philosophy, theories of free will and attribution of responsibility and is in line

with the reported high influence of cognitive and contextual factors such as personal definitions of control, on agency judgements (Synofzik, Vosgerau et al. 2008, Haggard 2017). If the explicitly reportable judgement of agency was identical with the implicit sub-conscious feeling of agency, applying the terms as defined by Synofzik, Vosgerau and Newen (Synofzik, Vosgerau et al. 2008), it needs to be considered that some traditional experimental designs in studies on agency and sensory attenuation might show conflicting results depending on the participants' conception of being an acting agent. Therefore, our study demonstrates that while the importance of choice for the formation of an effective SoA at least for some participants might not be too relevant for research on sensory attenuation, it still has interesting implications, as it suggests that one's personal intuition which is often used as the axiomatic foundation of theories of free will (see e.g. (Watson 2003)) cannot be assumed to be uniform.

However, according to the most common theories behind sensory modulation (self-specific and general predictive mechanisms (Kaiser and Schütz-Bosbach 2018)), the existence of an efference copy which would putatively also be present following a forced button press, should be sufficient.

Furthermore, it needs to be mentioned that one participant clearly showed the opposite pattern: they rated their agency highest in the passive and lowest in the active condition suggesting a mix-up of the conditions.

As suspected, there was no effect of agency on vection magnitude on the group level.

Direction choices

An interesting and unexpected finding was that participants have chosen forward-motion simulating optic flow significantly more often than backward in the choice condition. This finding might be explicable with the fact that humans are more used to radially-expanding optic flow in their daily lives (Diels and Howarth 2013). Walking backwards for more than just a few steps is the rather unusual case in daily life and requires more cognitive resources and attention and relies more on proprioception (Johansson, Lundin-Olsson et al. 2017) and might be accompanied by more stress. Another possible explanation could be that there is a directional asymmetry of motion perception as suggested by Berthoz et al. who also observed a difference in the postural responses: people tend to sway stronger forward than backward (around 25% more) which may be due to anatomical differences in e.g. the ankle configuration (Berthoz, Pavard et al. 1975). Those factors might have contributed to participants preferring the exposure to

radially-expanding optic flow. There was however no effect of direction on vection intensity, in line with findings by Guterman et al. who observed no effect in their main experiment (Guterman, Allison et al. 2012). They furthermore found forward translation simulating flow to be stronger compared to backward in a control experiment while it has also been reported that vection is stronger after exposure to contracting optic flow patterns (Bubka, Bonato et al. 2008). Those conflicting results might be attributable to differences in study designs and the generally hard quest to develop comparable optic flow stimuli for two opposite directions.

4.5 Limitations and further development

While our stimuli were known to be able to induce vection in participants in our lab setting, it is still a possibility that they might have rated the speed of the optic flow rather than their vection experience. Even though verbal reports in the informal debriefing suggested that they experienced vection, we cannot fully rule out that the speed judgement biased their vection reports. We therefore decided to include speed judgements after each trial in the next study for the following reasons: 1) the fact that they had to rate both could possibly prime them that vection and perceive speed are two different phenomena which might reduce the aforementioned bias if present, 2) while vection is a highly complex experience it might be possible to observe sensory modulation of speed perception to self-initiated optic flow.

After the successful proof-of-concept, we planned to increase the number of participants in Experiment 2 to boost the power of the design to elevate the chance to find sensory modulation if present, maybe also on a sub-group level in line with the findings by Reznik et al. who demonstrated that the intensity of the stimulus can determine whether the sensory consequences of self-initiated stimuli are perceived with enhanced or attenuated loudness (Reznik, Henkin et al. 2015). The threshold between subjective high - and low intensity might explain the absence of clear group level effects of agency on vection experience.

The analysis of the agency judgments revealed that the choice- and forward-instructed conditions are both suitable as a high agency active condition in comparison to passive exposure to optic flow which is in line with the intuition from the aforementioned studies. For practical reasons, we therefore decided to focus on the instructed condition (now called self-initiated) which allowed us to remove the keyboard which allowed the participants to sway more freely, reduced the risk for interference of the choice and the

button-press with EEG and decreased the number of different experimental conditions to have a higher number of trials for the relevant comparisons. To the same effect, we moved the computer mouse from the table which could be removed without the need for a keyboard, to the right thigh to further increase freedom of movement. Following the relocation of the mouse, the VAS was also rotated by 90° to allow more natural navigation on the VAS and consequently more reliable reporting. An additional advantage of focusing on forward vection was that it is the more natural stimulus compared to the radially-contracting pattern and participants seemed to prefer forward over backward (even though the reasons pointed out above are probably not comprehensive).

Another limitation of our study is the problem of central tendency during the first trials. Participants (mostly) have no prior experience with the abstract experimental optic flow. It is consequently quite hard for them to determine whether the optic flow they have just experienced is the fastest or most intense they will encounter during the experiment. While this poses a smaller problem for the judgement of vection intensity, it would be more problematic with speed judgements. We solved this by including practice trials prior to the actual experiment in Experiment 2 and 3 and show three reference speeds before each experimental block in the next study. To allow meaningful continuous speed judgements using a VAS, we expanded the 4 different speeds (20, 40, 60, 80) and used 80 different speeds (10-90) in the following experiments.

To reduce variance between the individual subjects, we decided to only include right-handed subjects in our following studies; research from our department showed that handedness might play a role in motion perception, especially when looking at brain activity (Dieterich, Bense et al. 2003, Kirsch, Boegle et al. 2018). In the following studies, we furthermore used a handedness questionnaire instead of the verbal assessments of handedness to make the inclusion criteria more objective and to identify and exclude ambidextrous subjects.

In line with the handedness questionnaire, we also started using formalized information sheets to make sure that every participant gets the same instructions and avoid biasing given the highly subjective nature and the importance of cognitive factors on vection experience and judgements as discussed above (Riecke 2009, D'Amour, Harris et al. 2021).

Given the growing literature on whether findings on sensory attenuation are attributable to self-specific and general predictive mechanisms (Kaiser and Schütz-Bosbach 2018),

we decided to introduce a random time interval between cue-offset and motion onset in the passive condition to also factor in differences in predictability of the stimuli which allows the observation of sensory attenuation independent of the underlying mechanisms. Furthermore, we decided to add a combined accelerometer-EEG setup to measure the postural and neurophysiological effects of the exposure to optic flow. This allowed us to look for both 1) objective markers of vection and 2) effects of agency and expectation at the physiological level.

One problem with the stimulus presentation during our experiment was that on some trials the faster speeds started slow and began to accelerate suddenly. Interestingly, anecdotal reports during the informal debriefing suggested that participants perceived stronger vection in such trials. This had two consequences for the design of the stimuli in the following experiment: Firstly, we switched to a pre-generated optic flow movie which had to be loaded only once at the beginning of the whole experiment and played this video with different speeds to avoid the speed bug. The second consequence was to play the optic flow movie following different acceleration profiles. This should typically increase the visuo-vestibular conflict and therefore delay vection onset latency or prevent vection onset fully according to the sensory-conflict theory by Zacharias and Young (Zacharias and Young 1981); the anecdotal reports of our participants however are in line with more recent research contesting the sensory-conflict theory and proposing that certain acceleration components in optic flow can actually facilitate vection induction (Palmisano, Allison et al. 2008, Palmisano, Kim et al. 2011, Palmisano and Riecke 2018).

4. Experiment 2

The Effects of Expectancy and Control on Vection Experience and Postural Sway in standing subjects: a combined Postural – and Electrophysiological Study.

4.1 Introduction

The aims of this study were two-fold: we wanted to overcome some of the limitations of the first experiment and deepen our understanding of the underlying neurophysiological processes giving rise to postural responses and more subjective phenomena such as vection and speed estimation. We modified the stimuli and setup as explained in the section above.

Concerning the behavioural results, we first expected that our accelerating stimuli were capable of inducing vection with a sufficient intensity and reliability even though the mean vection might be lower than in Experiment 1 due to the shorter duration of optic flow. We furthermore expected to find a high correlation between vection and perceived speed, however with different distributions based on the assumption that the speed of optic flow underlies and positively correlated with both the speed estimation and the vection experience (Brandt, Dichgans et al. 1973, Dichgans and Brandt 1978, Allison, Howard et al. 1999, Riecke 2010, Tamada and Seno 2015); at the same time participants are thought to report their real vection experience with a wider distribution because of the high inter-individual variance (Dowsett, McAssey et al. 2017). In line with the introduction to Experiment 1, we did not expect to find a clear effect of agency on explicit vection experience on the group level. In contrast, we anticipated finding some form of modulation of the evoked activity following exposure to optic flow. As discussed in the paper (Obereisenbuchner, Dowsett et al. 2021) and in Chapter 1, this influence was thought to be mainly a reduced ERD over parieto-occipital channels in the self-initiated compared to the passive condition. Additionally, we predicted neurophysiological differences in the activity recorded over early visual cortex and motion sensitive areas dependent on the speed of optic flow and the intensity of vection that participants experienced (see Chapter 1 for a more in-depth overview on the relevant areas. An increase in the N2 component preceding vection experience has previously been described (Keshavarz and Berti 2014, Berti, Haycock et al. 2019), we therefore expected to find a larger negative deflection at around 130 - 250 ms in high vection trials, based

on the discussion by Vilhelmsen et al. (Vilhelmsen, van der Weel et al. 2015), which would also be expected for higher speeds of the optic flow (Maruyama, Kaneoke et al. 2002, Heinrich 2007). Based on the extensive literature demonstrating alterations in postural control during vection perception, e.g. by Palmisano et al. (Palmisano, Allison et al. 2015), we expected to find increased postural instability or sway magnitude (Kuno, Kawakita et al. 1999, Fushiki, Kobayashi et al. 2005, Tamada and Seno 2015), at around the time of vection onset respectively increased postural instability in trials with higher vection. On the basis of work by Guerraz et al., we predicted reduced postural responses to self-initiated optic flow (Guerraz, Thilo et al. 2001). However, most studies used longer trials and / or other methods to measure postural sway, therefore the ground on which those predictions are build was not as firm as the neurophysiological hypotheses.

4.2 Methods

Participants

21 healthy, right-handed (mean laterality index: 83.2; mean age: 22.9±3.3, range: 18 - 31; 11 females) adults with no history of neurological or psychiatric disorders and normal or corrected to normal vision participated in our study. Two experiments had to be stopped due to the occurrence of high levels of symptoms suggestive of motion sickness such as paleness, sweating, nausea, eye strain and general discomfort (Golding and Gresty 2015, Bertolini and Straumann 2016, Keshavarz, Murovec et al. 2021) and one fainted. The participants were excluded from all further analyses. All subjects provided written and informed consent and were financially compensated for their participation.

Procedure

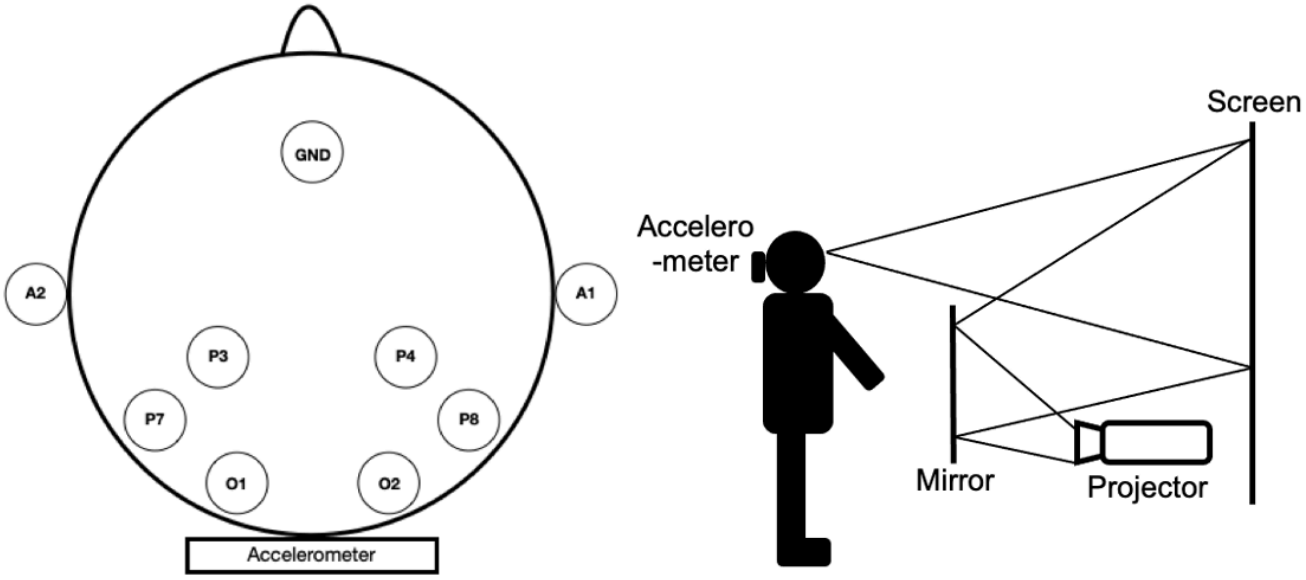

Figure 18: Montage of EEG electrodes, the accelerometer (left) and participants' posture relative to the screen (right). The eye-screen distance was 1.15 m and the visual angle 90° x 60°. Modified from the published paper (Obereisenbuchner, Dowsett et al. 2021).

After the set up was completed, each participant stood in front of the display, in a comfortable position with their hands to their sides and the computer mouse in their right hand. The experiment started with a calibration period where participants had to follow instructions and perform certain body-movements: moving down / up, leaning to the left / right and forward / backward.

The experiment consisted of 240 trials organized in 6 active and 6 passive blocks of 20 trials each in randomized order. At the beginning of each block, the reference speeds were presented again. After each trial, participants were first asked to rate the speed of the optic flow relative to the three reference speeds on a vertical VAS, followed by their vection judgement on another vertical VAS.

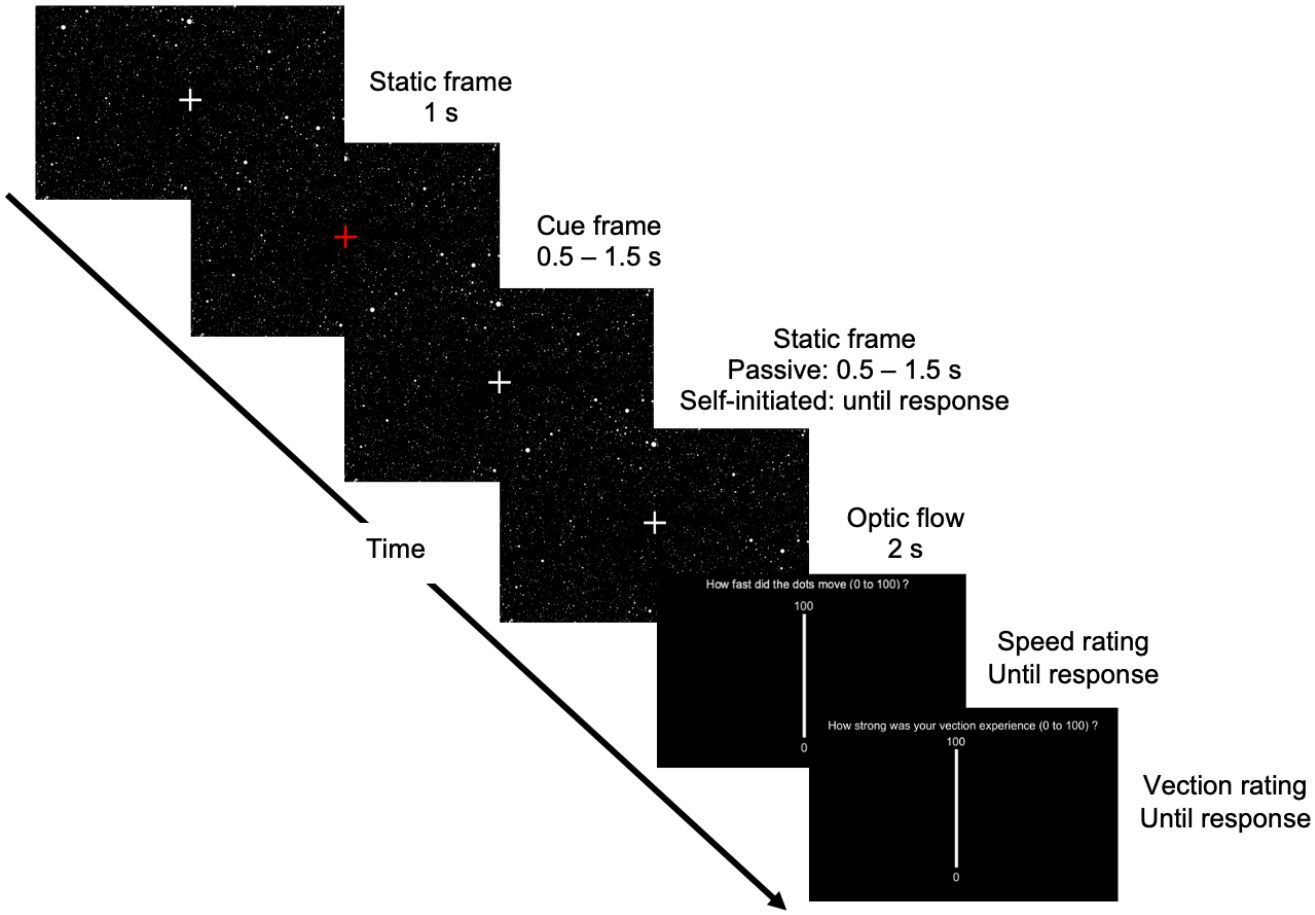

Figure 19: Task schematic showing the two agency conditions. On self-initiated flow trials, the participants initiated the flow onset by pressing a button. On passive flow trials the flow was started by the computer, and they did not press a button. Modified from the published paper (Obereisenbuchner, Dowsett et al. 2021).

4.3 Results

Behavioural results

The mean vection rating (Figure 20) was 40.9 ± 4.3 out of 100 on the VAS. One participant reported to feel no vection at all. There were no significant differences, neither between reported vection in self-initiated (41.6 ± 4.5) compared to passive (39.9 ± 4.3) trials (t_{18} = 0.94, p > .05, Figure 21) nor between the absolute speed estimation error in self-initiated (9.3 ± 0.9) compared to passive (9.2 ± 0.7) trials (Z = 0.02, p > .05, Figure 22). Figure 23 shows the relationship of the correlation coefficients of the presented optic flow speed and vection ratings and the speed estimations; the figure demonstrates that there generally is a correlation of Spearman's ρ > .5 with the speed estimations while the distribution of the correlation coefficients with the vection ratings is much wider and for some participants even negative. The mean of the correlation

between vection ratings and speed judgements however suggests a positive correlation *(ρ* = .57). While not overtly assessed, two participants' experiments had to be stopped due to vegetative symptoms with paleness, sweating and nausea combined with eye strain and general discomfort. One of those participants collapsed probably due to low blood pressure. Those vegetative disturbances could be related to either the rather long standing duration or motion sickness (an overview of the typical symptoms can be found in Chapter 1). Informal debriefing of the other participants showed that lower levels of motion sickness – like symptoms were not uncommon but were not further quantified in this study.

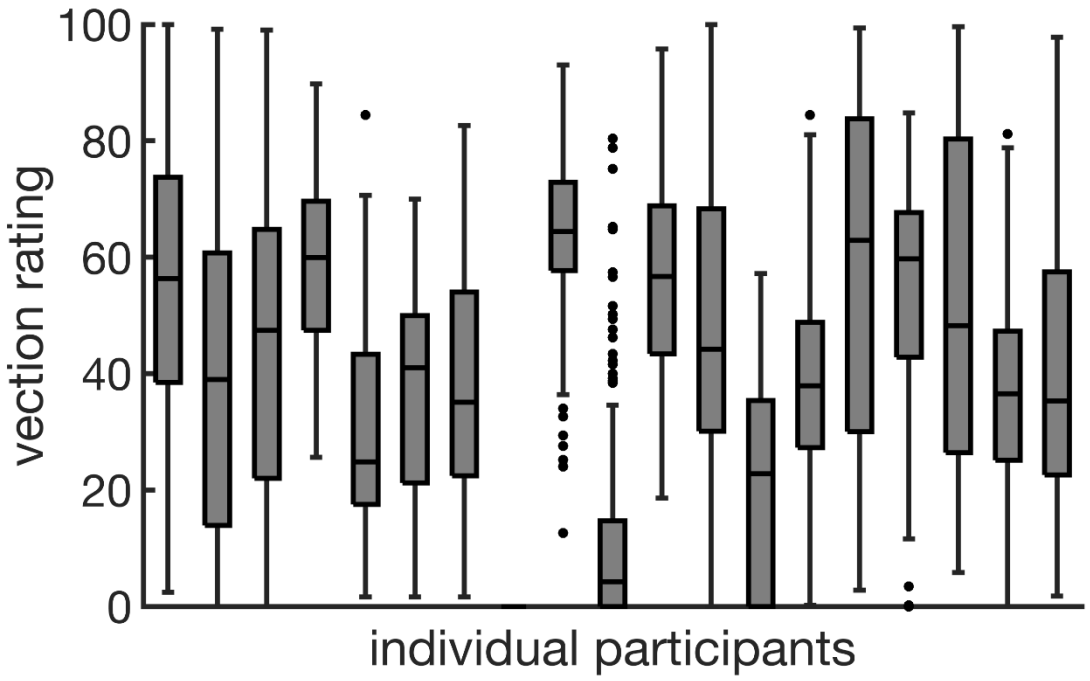

Figure 20: Individual patients vection ratings and variability over the course of the experiment. Horizontal lines inside the boxes show the median of vection ratings. Boxes show the interquartile range. The whiskers show the highest and lowest non-outlier ratings (quartiles defined as 0.75 respective 0.25 quartiles).

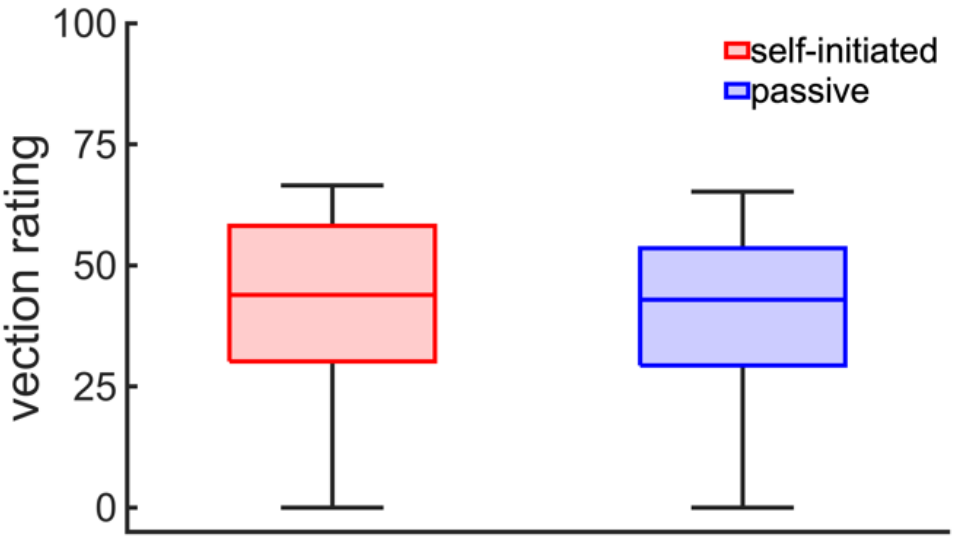

Figure 21: Comparison of the rating of the vection experience in self-initiated (red) and passive trials (blue). The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. The vection ratings showed high inter-individual variability and did not differ between conditions.

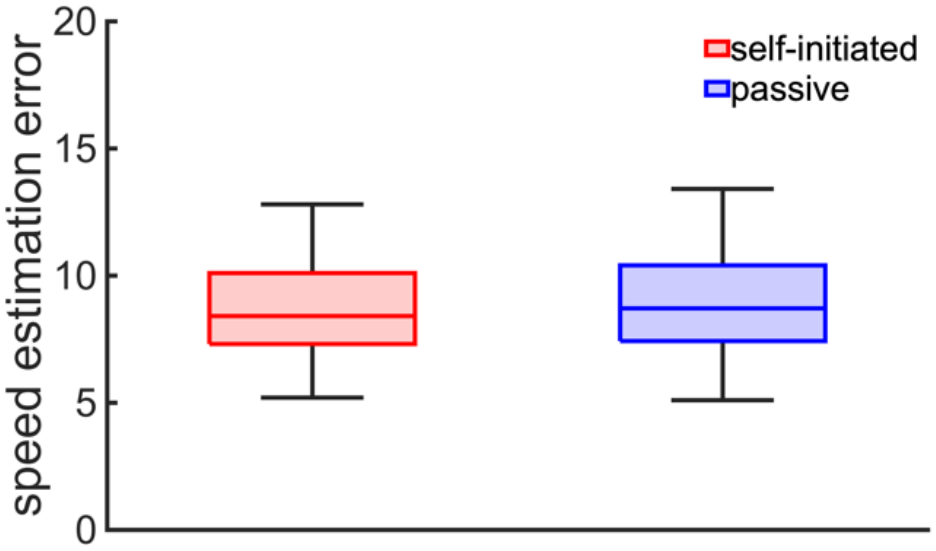

Figure 22: Comparison of the speed estimation error, defined as the absolute difference between presented speed and estimated speed in self-initiated (red) and passive trials (blue). The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. No outliers. The error did not differ between conditions.

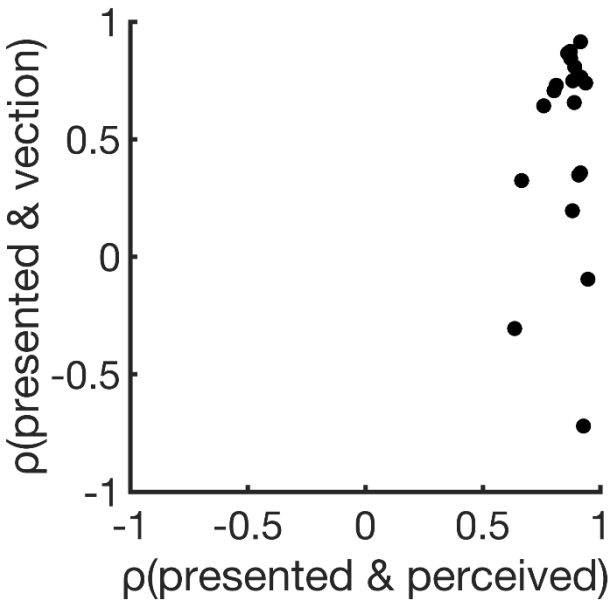

Figure 23: Each point shows the correlation coefficients for the comparison vection rating and presented speed (ordinate) and speed estimation and presented speed (abscissa) of one participant. Note that the distribution along the ordinate is much wider than the distribution along the abscissa.

Accelerometer results

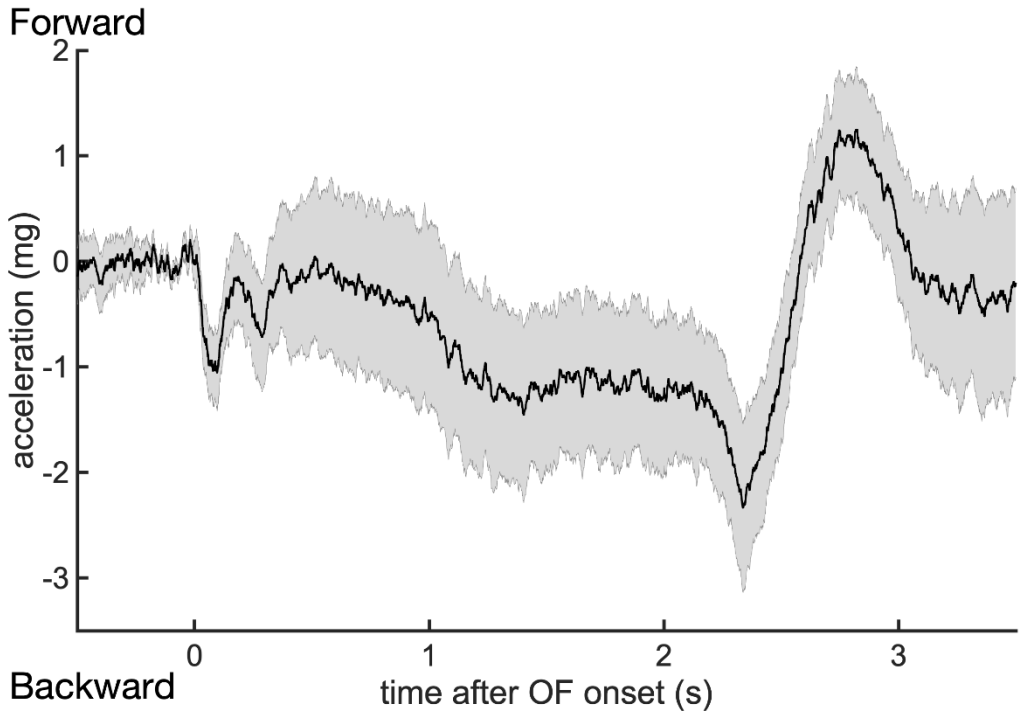

Figure 24: Visually induced postural sway responses for all conditions pooled to allow for the identification of interesting features to inspire hypothesis-driven analysis. The shaded area represents the standard error of the mean. The VIPR shows first a backward acceleration component at around the time of optic flow onset followed by proceeding backward acceleration until optic flow offset. The offset is followed by a peak in backward acceleration followed by a strong forward acceleration which reaches baseline again at approximately 3 s after optic flow onset. These last components are probably due to the speed judgements on the vertical VAS.

Figure 24 shows the VIPR of all conditions pooled. The first fast backward sway components start directly after optic flow onset and last until approximately 500 ms. Those components are followed by a slower postural response which resembles leaning backwards and which peaks after the optic flow reaches its maximum speed and enters the phase of continuous speed. The offset of the optic flow is followed by a short increase in backward acceleration before participants start leaning forwards again until they reach the start position again at around 1.5 s after offset. It is noteworthy that the sway after offset might be confounded by the speed rating as the 1 s of presentation of the static frame was not introduced until Experiment 3.

We first analysed the overall sway defined as the sum of the absolute sway over the whole time when the optic flow was present (0-2000 ms after optic flow onset). Figure 25 shows the visual evoked postural responses to self-initiated and passive. The overall sway in self-initiated (4330.0 mg) and passive (4495.6 mg) was not significantly

different (Z = -0.93, p > .05). We then tested whether the fast backward sway component was different dependent on the agency condition (Figure 26); and indeed, the amplitude of the component was significantly larger in the self-initiated condition (Z = -2.13, p < .05). Closer visual inspection of Figures 24 and 25 shows that the sway component in the pooled VIPR can actually mainly be attributed to the first backward sway component in the self-initiated condition which is almost absent in the passive condition. In the next step, we looked for differences in overall sway between high - and low vection trials (Figure 27); because of the high inter-individual sway differences, we only considered participants with ≥ 20 high - and low vection trials to avoid bias introduced by e.g. one participant who generally shows high postural responses but noticeable low vection. The number of subjects considered in the vection VIPR is therefore reduced to 16 instead of 19. However, there was no significant difference observable (Z = 0.50, p > .05).

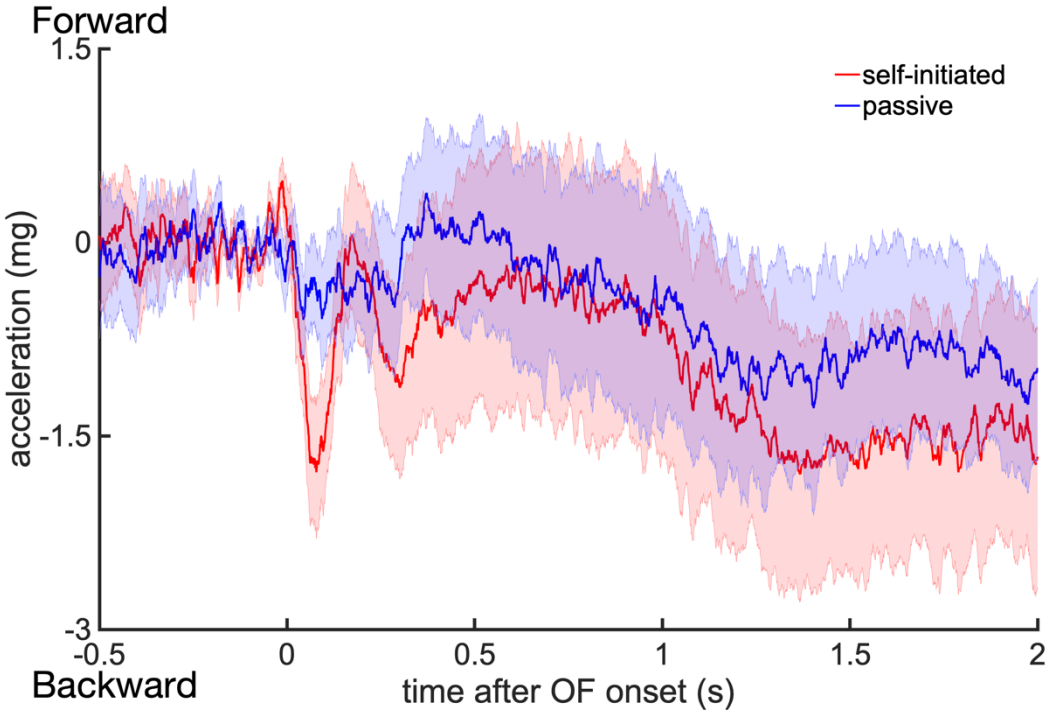

Figure 25: Visually induced postural sway responses on self-initiated (red) and passive trials (blue). The shaded area represents the standard error of the mean. The first backward acceleration component at around the time of optic flow onset is not present in the passive conditions. Except for this component, the two VIPRs differ only minimally.

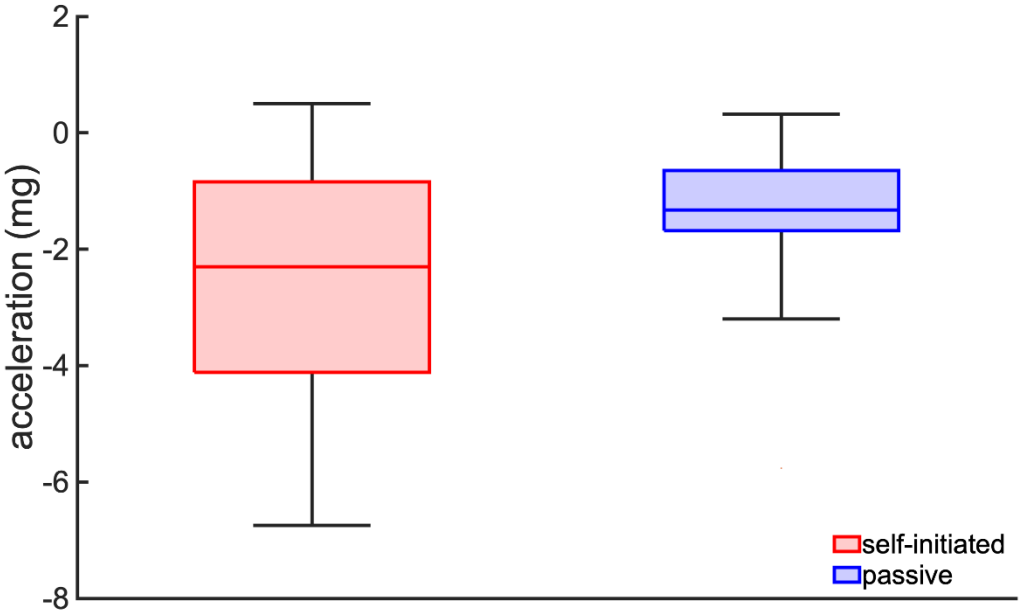

Figure 26: Isolation of the peak backward acceleration in the time interval 0-100 ms after optic flow onset in self-initiated (red) and passive (blue) trials. The horizontal line in the box plot shows the median, the box marks the interquartile range, and the whiskers show the highest and lowest non-outlier values. No outliers. The peak acceleration in the self-initiated condition was significantly higher.

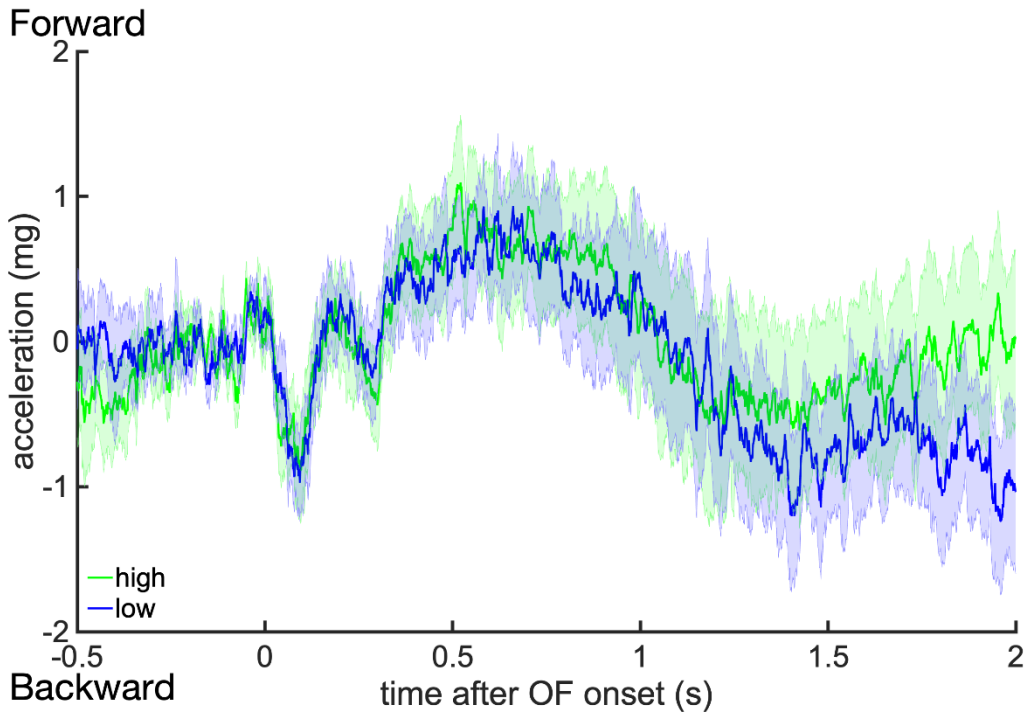

Figure 27: Visually induced postural sway responses for trials in which participants rated their vection experience to be high (green) and low (blue). Shaded area represents the standard error of the mean. The VIPRs seem to begin to differ after approximately 1.5 s.

Interestingly, it seems as if the VIPRs in high and low vection trials diverge at around 1.5 s after optic flow onset. We therefore repeated the analysis and plotted additional 1.5 s in Figure 28 which shows that participants' sway patterns are very different after optic flow offset.

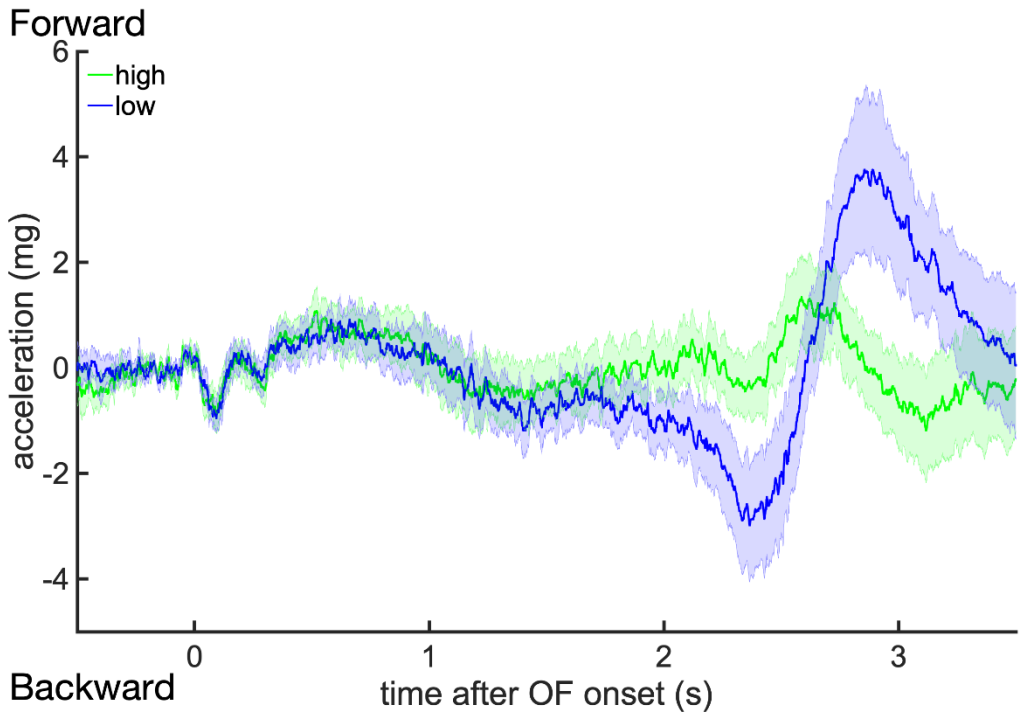

Figure 28: Visually induced postural sway responses for trials in which participants rated their vection experience to be high (green) and low (blue). Shaded area represents the standard error of the mean. The VIPRs begin to differ after approximately 1.5 s and diverge impressively after the end of optic flow (after 2 s). The head sway after the offset is probably due to the speed judgement.

While this might seem surprising, it can probably be attributed to postural adjustments during the VAS ratings: participants who give very high or low ratings towards the extremes of the VAS might move their head to prepare for the response towards the upper or lower border of their field of view. We therefore also looked at the elongated VIPRs for fast and slow presented speeds. And indeed, the figure (Figure 29) looks very similar, which in turn is not surprising given the high correlation of presented speed and vection rating. What is interesting however, is the fact that it looks as if the two curves deviate almost directly after the optic flow enters the continuous phase, suggesting that participants might have (unconsciously) adjusted their posture during the trial in preparation of the response following the offset as soon as they have perceived the needed information for their judgement.

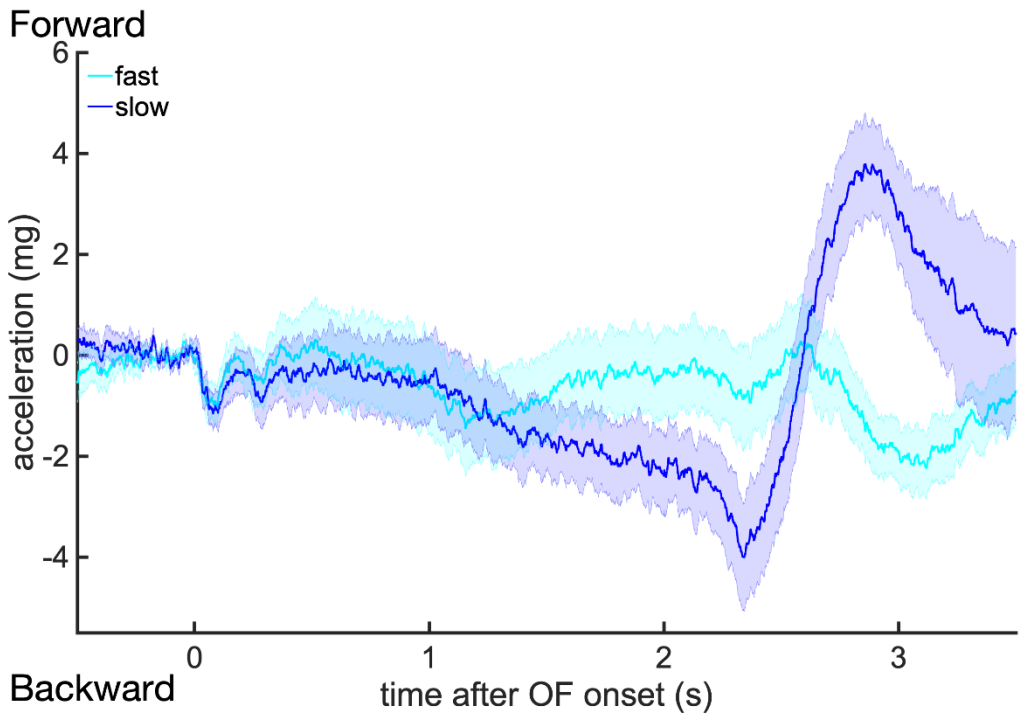

Figure 29: Visually induced postural sway responses for faster than average (light blue) and slower than average trials (dark blue). Shaded area represents the standard error of the mean. The VIPRs begin to differ after approximately 1.5 s and diverge even stronger than the vection VIPRs after the end of optic flow (after 2 s). The head sway after the offset is probably due to the speed judgement.

Event-related potentials

In line with the VEPs presented by earlier studies (Maruyama, Kaneoke et al. 2002, Heinrich 2007, Vilhelmsen, van der Weel et al. 2015), the main ERP feature we observed was a negative deflection peaking at around 250 ms after optic flow onset. We performed paired-sample two-tailed t-tests if appropriate given the assumptions of normality and / or equality of variances, and Wilcoxon Signed Rank tests otherwise, to compare the amplitude of the negative deflection in trials with high - and low vection ratings (Figure 30) as well as in trials with fast (speed ≥ 50) and slow optic flow trials (speed< 50) (Figure 31): because of the high inter-individual variability in vection perception, we only considered participants with both ≥ 20 high - and low vection trials to avoid bias. The vection VEP is therefore calculated with a reduced number of participants of 16 instead of 19. We found no significant difference for neither the vection comparison (all $p > .05$) nor for speed (all $p > .05$).

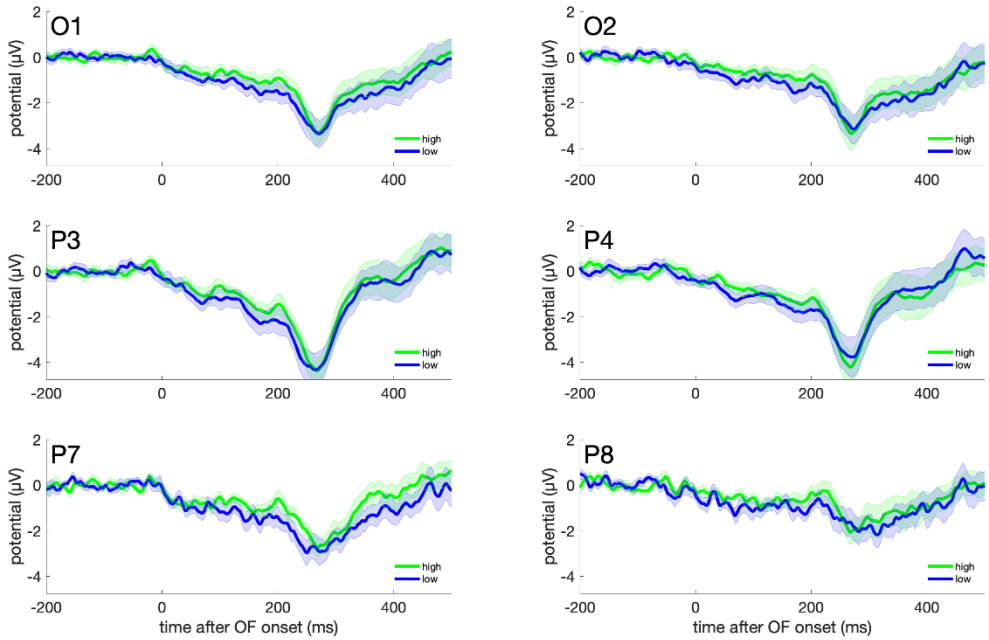

Figure 30: ERP for trials in which participants rated their vection experience to be high (green) and low (blue) for all parietal and occipital channels. Shaded area around the ERPs represents the standard error of the mean. The N2 component in the interval 200-300 ms is the most prominent feature.

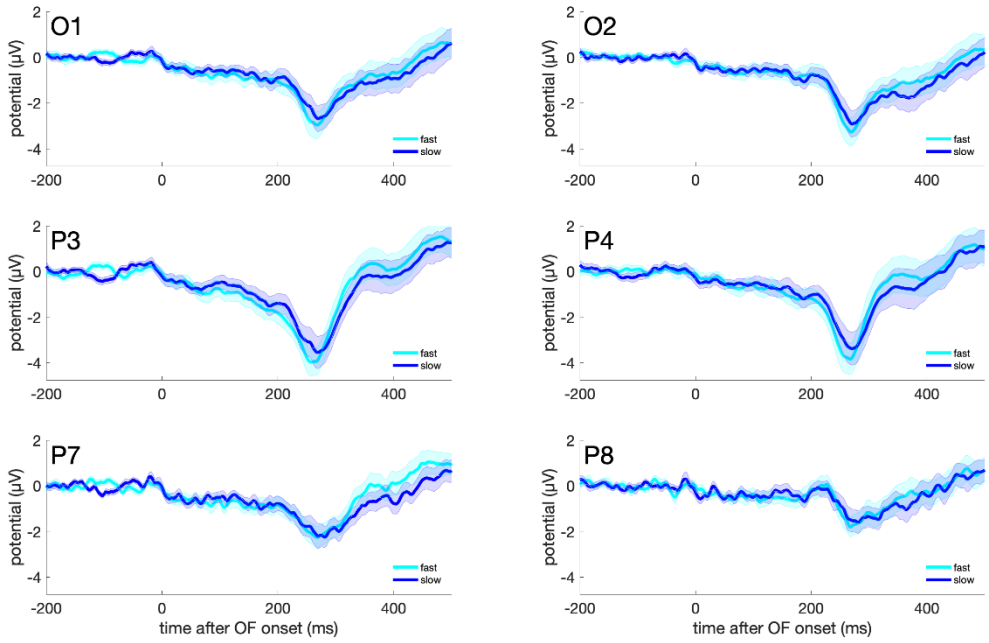

Figure 31: ERP for faster than average (light blue) and slower than average trials (dark blue) for all parietal and occipital channels. Shaded area around the ERPs represents the standard error of the mean. The N2 component in the interval 200-300 ms is the most prominent feature. Note that there is no apparent difference in the amplitudes.

In the next step, we looked at our focus of interest, namely the comparison of the ERP elicited by self-initiated compared to passive optic flow. Visual inspection of the ERPs shows that the two curves diverge from the moment the optic flow begins, with a large negative deflection plateauing at around 150 ms, the time which has been associated with the neurophysiological correlate of optic flow (van der Meer, Fallet et al. 2008, Agyei, Holth et al. 2015). The negative component at around 250 ms also clearly deviate, but the main effect seems to start earlier. We decided therefore to compare the amplitude in the time interval 130-170 ms in the two agency conditions which was also in line with previous research (Berti, Haycock et al. 2019). The amplitude was significantly higher in self-initiated for all channels: O1 ($Z = -3.54$, $p \leq .001$), O2 ($Z = -3.54$, $p \leq .001$), P3 ($Z = -3.58$, $p \leq .001$), P4 ($Z = -3.42$, $p \leq .001$), P7 ($Z = -3.66$, $p \leq .001$) and P8 ($Z = -2.90$, $p \leq .01$).

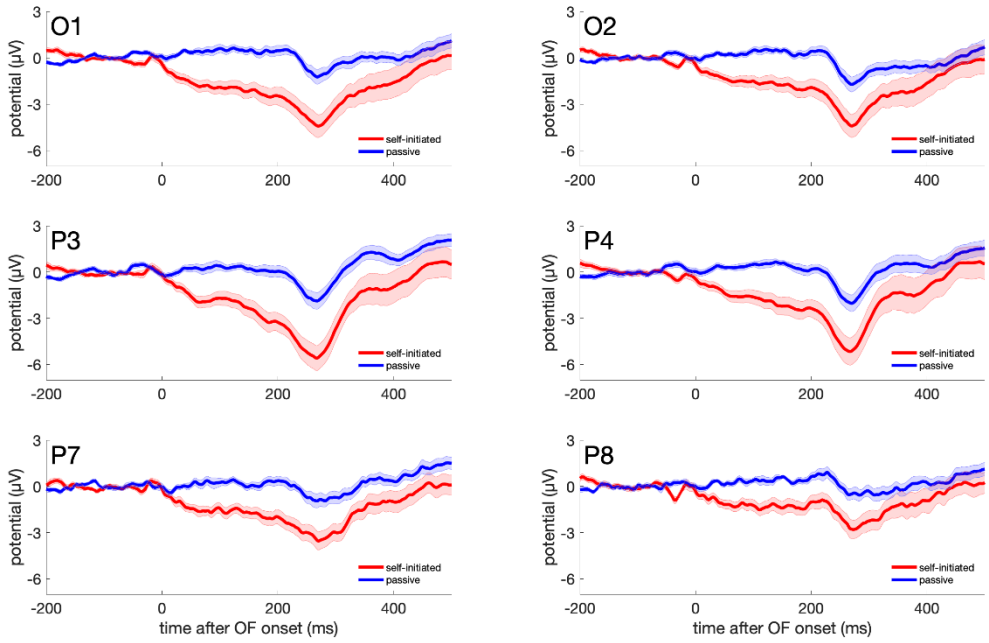

Figure 32: ERP for self-initiated flow (red) and passive flow (blue) for all parietal and occipital channels. The shaded area around the ERPs represents the standard error of the mean. Between 130–170 ms, we observed a prominent negative deflection in the self-initiated condition.

Event-related desynchronization

We looked at the changes in alpha power relative to pre-trial baseline (dB-scaled as described in Mike X. Cohens book on EEG data analysis (Cohen 2014)) using paired-sample two-tailed t-tests to compare the mean power during the trial (0 – 2000 ms after optic flow onset) relative to the baseline, between conditions, first during high - and low

vection trials (Figure 33); and indeed, we found a significantly stronger ERD during high vection trials for channels O1 (t_{15} = -2.99, p ≤ .01), O2 (t_{15} = -2.30, p ≤ .05) and P4 (t_{15} = -2.23, p ≤ .05) and marginally-significant for channel P3 (t_{15} = -2.10, p = .053). Next, we checked whether this effect might be attributable to the higher optic flow speed due to the high correlation between presented speed and vection experience (see above). And indeed this seems to be possible: the ERD is significantly stronger in fast trials (Figure 34, speed ≥ 50) for channels O1 (t_{18} = - 2.13, p ≤ .05), O2 (t_{18} = -2.11, p ≤ .05), P3 (t_{18} =-3.03, p ≤ .01), P4 (t_{18} = -2.75, p ≤ .05) and P8 (t_{18} = -3.43, p ≤ .01); no significant difference was observable for channel P7 (t_{18} = -1.34, p > .05).

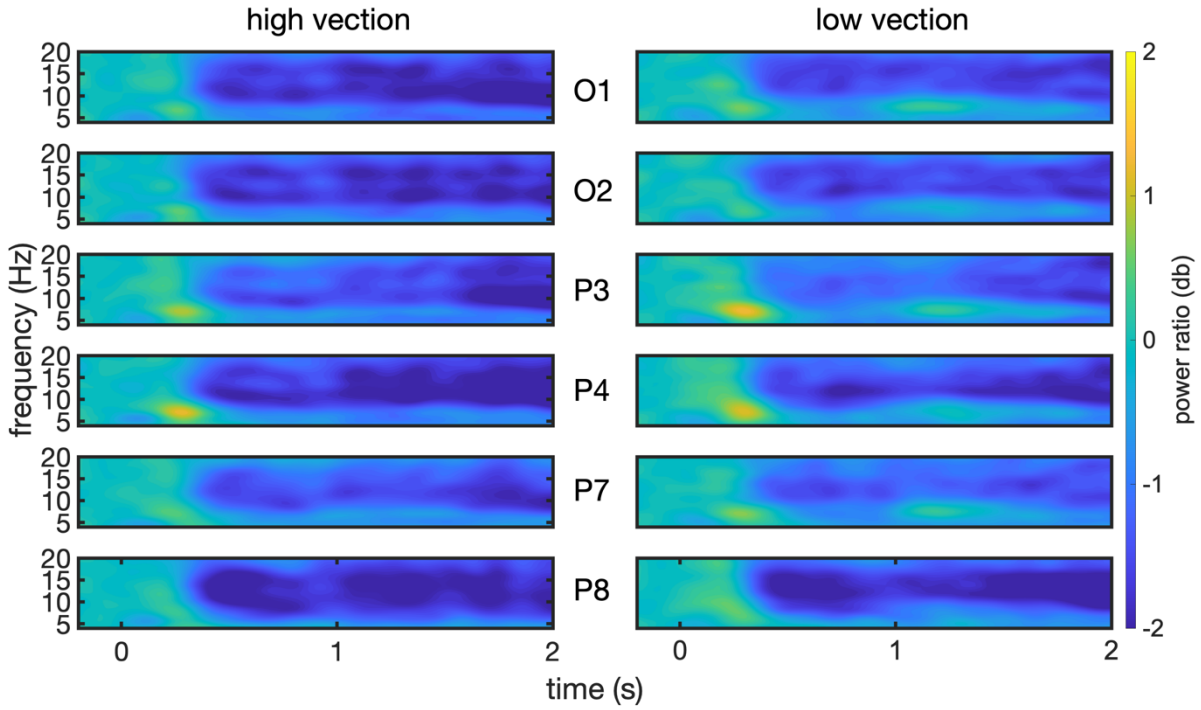

Figure 33: Power spectra (dB-scaled power ratios) relative to optic flow onset in trials in which participants rated their vection experience to be high (left column) and low (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric. The colours encode the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Event related desynchronization in the alpha band (blue) is evoked by optic flow and seems to be stronger during high vection trials.

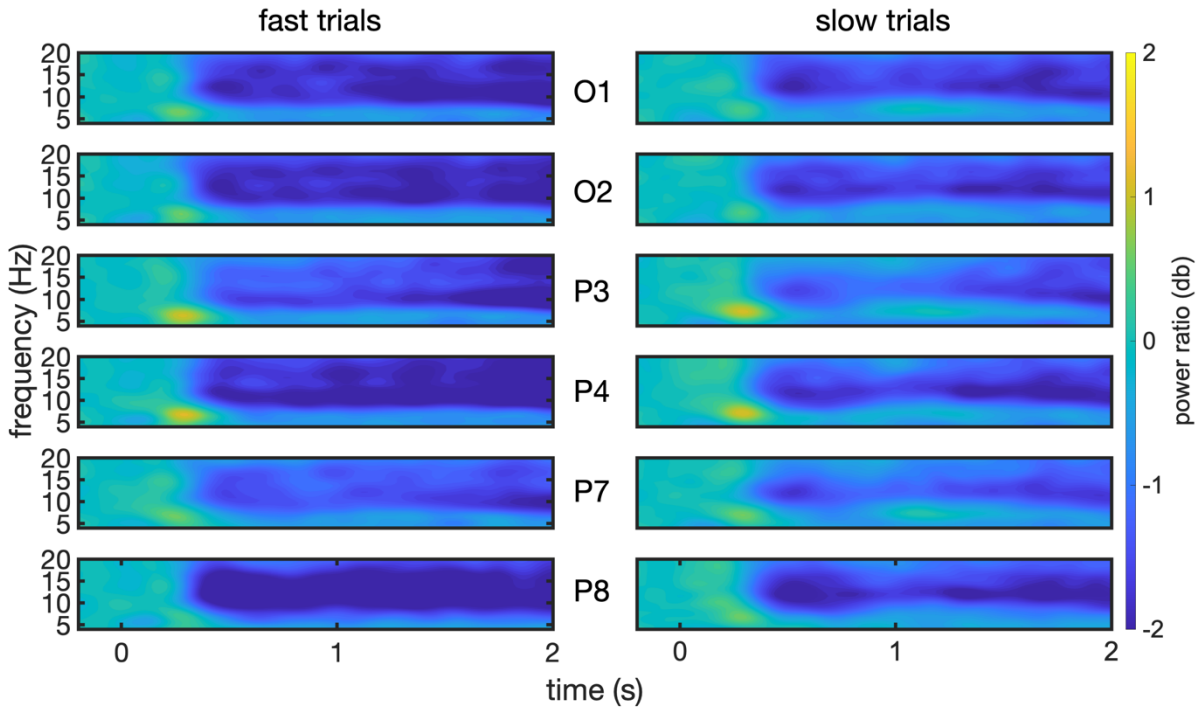

Figure 34: Power spectra (dB-scaled power ratios) relative to optic flow onset in faster than (left column) and slower than average trials (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric. The colours encode the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Event related desynchronization in the alpha band (blue) is evoked by optic flow which seems to be markedly stronger during fast trials.

In the last step, we looked at our main question, namely whether there is an effect of agency condition on the neurophysiological signature of the perception of optic flow. We compared the magnitude of the ERD in self-initiated and passive. As predicted, we found the ERD to be significantly reduced in the self-initiated condition for all channels: O1 ($t_{18} = 4.54$, $p \leq .001$), O2 ($t_{18} = 3.30$, $p \leq .01$), P3 ($t_{18} = 5.46$, $p \leq .0001$), P4 ($t_{18} = 4.12$, $p \leq .001$), P7 ($t_{18} = 5.17$, $p \leq .0001$) and P8 ($t_{18} = 3.56$, $p \leq .01$).

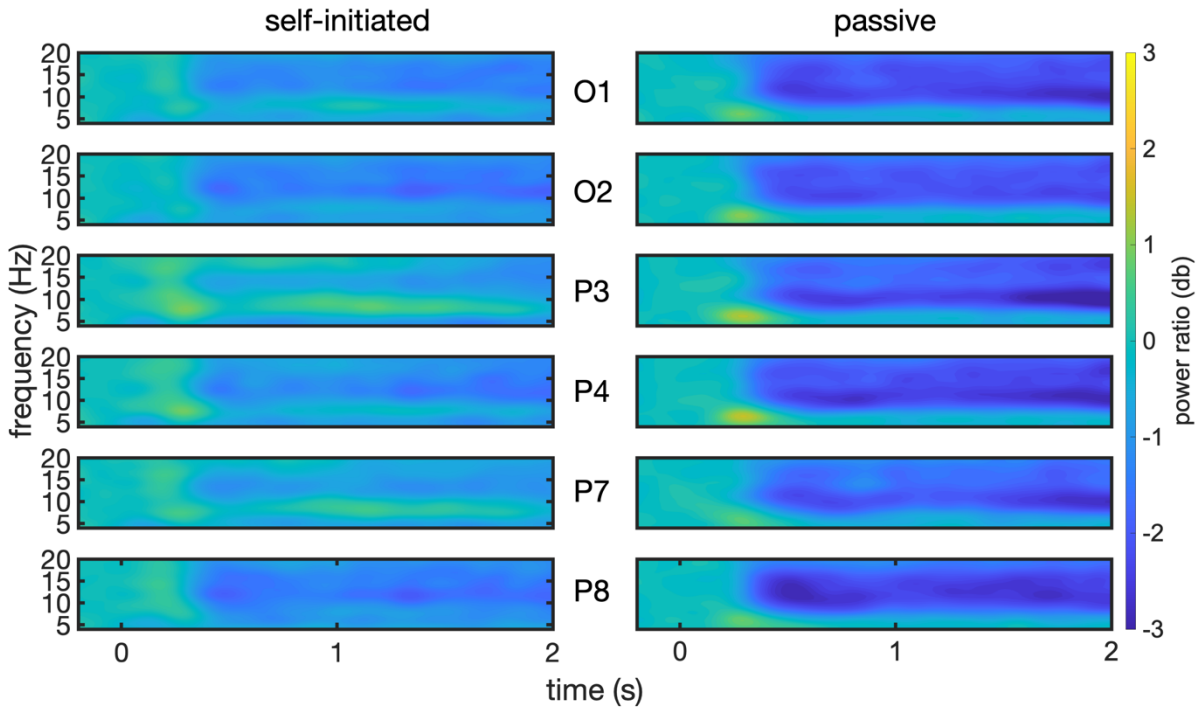

Figure 35: Power spectra (dB-scaled power ratios) relative to optic flow onset in the self-initiated (left column) and passive condition (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric. The colours encode the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Event related desynchronization in the alpha band (blue) is evoked by optic flow which was inhibited in the self-initiated compared to the passive condition for all channels.

4.4 Discussion

Experimental Design

We asked our participants during the informal debriefing whether the computer mouse on their thigh and the response on the vertical VAS felt natural and intuitive for them and only got positive feedback.

Behaviour

To address one of the limitations of Experiment 1, we analysed the relationship of speed estimations and vection ratings to evaluate whether participants might rate the optic flow speed instead of their vection experience; it is well known that faster optic flow tends to induce stronger vection (Tamada and Seno 2015). Therefore, as long as the slow trials are also able to induce at least some vection, one would expect to find a strong correlation between vection ratings and both perceived and actual speed of optic flow. If one wanted to show that vection ratings and speed estimates are based

on dissociable subjective experiences except for the influence of actual speed on both, one would either have to show that they can be modulated independently using a specific experimental design or that the distribution of the two ratings is different. Indeed, Figure 23 demonstrates that vection has a much wider distribution with some participants even showing a negative correlation between presented speed and vection while speed estimates correlated positively with presented speed for each participant. For other aspects on the vection inducing capability of our stimuli see the discussion of our paper and the general discussion.

Event-related potentials

The form and timing of the VEP in this study closely resembled the findings published in our paper on Experiment 3 (Obereisenbuchner, Dowsett et al. 2021) in sitting participants as well as the motion-onset VEPs described by Maruyama et al. (Maruyama, Kaneoke et al. 2002, Heinrich 2007) although they underlie considerable inter-individual differences of the overall shape and the N2 latency (Kubová, Kuba et al. 1990). Against our expectations, we did not observe any significant differences of the N2 amplitude either for varying vection intensities nor for different speeds. This will be discussed in more detail in the general discussion. As predicted and in line with the claim that there is sensory attenuation on the physiological level in the visual motion processing domain, we found a large negative deflection spanning all parieto-occipital channels, peaking in the time interval 130-170 ms, just preceding the N2 component which is only present whenever the stimuli were self-initiated; to the best of our knowledge, this component has not been described before. The putative source and function of this deflection is discussed in more detail in the paper and the general discussion.

Event-related desynchronization

As expected, we observed a strong bilateral ERD in all parieto-occipital channels during optic flow (Ehinger, Fischer et al. 2014, Vilhelmsen, van der Weel et al. 2015, Palmisano, Barry et al. 2016) which was inhibited when self-initiated; this is in line with the postulated sensory attenuation of visual motion perception on the neurophysiological level (Obereisenbuchner, Dowsett et al. 2021) and will be discussed in more detail in the general discussion. Additionally, we found a significantly stronger ERD in high -

compared to low vection trials which is in line with reports that cortical activity is increased during vection experience (Keshavarz and Berti 2014, Palmisano, Allison et al. 2015). However, it does probably not represent the cortical correlate for vection experience but rather results from the different optic flow speeds. This is more likely as the increased ERD is more widespread and more consistent for higher-than-average speeds and given the high correlation of optic flow speed and perceived vection intensity. It can however not be ruled out that the interaction is mediated the other way around and that the differences in the ERD result from the higher vection experience in faster trials or that the two effects synergistically increase activity in motion sensitive cortical areas.

Posture

In accord with the argumentation followed in the publication (Obereisenbuchner, Dowsett et al. 2021), the first backward sway component directly following the onset of optic flow is probably due to the button press. The absence of a motor-only control condition however prevents the verification of this claim. Apart from this, there were no differences in the postural responses between the self-initiated and the passive condition observable. We found no differences of the sway during the trial neither for different vection intensities nor for varying optic flow speeds. By contrast, the VIPRs differed considerably, first only visually and not ascertained by statistical analysis during the continuous optic flow stage and mainly after the end of optic flow as shown by the prolonged plots. Those responses probably do not result from offset – or aftereffects of optic flow, which should not start as early as during the exposure. They are also substantially larger than the VIPRs and therefore are probably not attributable to the exposure to optic flow. The most probable reason, as already implied in the results section, also has some interesting implications. Due to the design of the experiment, there was no static frame following the end of optic flow and the stimuli thus disappeared suddenly after 2 s with the next frame directly showing the VAS for the speed estimation. The highest and lowest possible ratings (0 and 100 respectively) were placed toward the borders of the field of view. One can therefore assume that participants might have moved eyes and head to fixate the point on the VAS where they subsequently gave their speed judgement. The amplitude of the postural adjustment is much stronger for slow respective low vection trials which implies that participants tended to move their head more to see objects in the lower part of their visual field

given that the middle of the VAS was in the height corresponding to the placement of the fixation cross which was adjusted to be right in front of their forward-looking eyes in a comfortable standing position before the beginning of the experiment. Another explanation would be that the custom-made glasses did not restrict the vertical field of view symmetrically. Independent of the cause for the asymmetry in the postural response, the most interesting aspect of this auxiliary finding is the fact that it seems to start already during the second phase of the optic flow. As this phase consists of continuous radially-expanding optic flow, it is per se not relevant to give a correct speed estimation. After 1 s of exposure, participants already know the maximum speed. One interpretation of this might be that participants either consciously or subconsciously prepared for their response during optic flow. As pointed out by Warren, 300 ms are enough to give quite reliable heading judgements (Warren 1995). Therefore, it is quite possible that speed estimations might also start being prepared within 500 ms after the perception of the relevant information giving rise to this unexpected finding.

4.5 Limitations and further development

Our main aims behind a modified design for Experiment 3 was to evaluate the credibility of our strong neurophysiological findings. The first step was therefore to include a button-press-only control condition to be able to isolate the motor action (button-press-only) and the sensory input (passive, optic flow only) and compare both to the combined condition of interest (self-initiated, motor + optic flow). If the weakened ERD and the negative deflection in the ERP (130-170 ms after optic flow onset) were also present in the control condition, then the effects should rather be attributed to the motor command per se and not to the modulation of the perception of self-initiated visual self-motion cues. Another important limitation of Experiment 2 was the absence of data on e.g. the duration a participant waited until they pressed the button in the self-initiated condition which would have been needed for control analyses as the ones done in the paper. While Experiment 2 was thought to be an exploratory study as well, we needed to focus more on the data quality of especially the neurophysiological data to evaluate whether the differences between the amplitude of the negative deflection are due to a real effect. We therefore decided to develop an experiment with half the trials under typical EEG conditions (e.g. sitting participants, chin rest) and the second half with a focus on the postural responses (no chin rest). This design has the advantage that it reduces the risk of our results just being artifacts from the mobile recording setup to

the level of a ‘normal’ EEG study. The disadvantage of this design is that the number of trials per condition is reduced. To allow the formation of meaningful ERPs, we decided to shorten the trials as much as possible while increasing the total number of trials. We hence removed the speed judgements and included the VIMS ratings at the end of each block instead. This saved us approximately 1 - 2 s per trial. It furthermore reduced the risk of the speed estimation biasing the vection rating. To avoid postural responses such as the one which we attributed to a preparation of the speed estimation, we presented the static frame for 1 s after the end of optic flow and before the vection rating. We additionally designed the experiment for sitting participants because this comes with several opportunities: we could increase the overall recording duration, and thus include more trial blocks, because it is much more comfortable and at the same time sitting is thought to reduce the noise of the EEG signal. It furthermore might mitigate the problem that two participants almost fainted during Experiment 2, probably due to a combination of the long standing-duration and VIMS. A similar phenomenon has also been reported in a very early vection study by Lestienne in which three participants out of 30 fainted and subjects repeatedly described an “intense, disturbing sensation”; both was associated with the exposure to high image velocities (Lestienne, Soechting et al. 1977). To reduce the risk of vegetative reactions further, we introduced the FMS rating (Keshavarz and Hecht 2011) at the end of each block to: 1) find out if the problems are related to motion sickness in the first place, 2) to be more aware what type of subjective experience, e.g. vection or VIMS we are actually measuring (Keshavarz, Riecke et al. 2015), and 3) to have a parameter to be able to intervene before participants feel too uncomfortable and increase e.g. the break duration as appropriate. As long as we do not apply the FMS or another measure of VIMS, all our assumptions on motion sickness will just be speculative or anecdotal reports. The downside of the change from standing to sitting was that our postural findings from Experiment 2 were only of very limited transferability; in fact postural stabilization and - control seem to differ between different postures as discussed in Chapter 1 based on findings by Fujimoto and Ashida (Fujimoto and Ashida 2020).

5. Experiment 3 – publication

NEUROSCIENCE
RESEARCH ARTICLE
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Self-initiation Inhibits the Postural and Electrophysiological Responses to Optic Flow and Button Pressing

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Abstract—As we move through our environment, our visual system is presented with optic flow, a potentially important cue for perception, navigation and postural control. How does the brain anticipate the optic flow that arises as a consequence of our own movement? Converging evidence suggests that stimuli are processed differently by the brain if occurring as a consequence of self-initiated actions, compared to when externally generated. However, this has mainly been demonstrated with auditory stimuli. It is not clear how this occurs with optic flow. We measured behavioural, neurophysiological and head motion responses of 29 healthy participants to radially expanding, vection-inducing optic flow stimuli, simulating forward transitional motion, which were either initiated by the participant's own button-press (''self-initiated flow'') or by the computer (''passive flow''). Self-initiation led to a prominent and left-lateralized inhibition of the flow-evoked posterior event-related alpha desynchronization (ERD), and a stabilisation of postural responses. Neither effect was present in control button-press-only trials, without optic flow. Additionally, self-initiation also produced a large event-related potential (ERP) negativity between 130–170 ms after optic flow onset. Furthermore, participants' visual induced motion sickness (VIMS) and vection intensity ratings correlated positively across the group – although many participants felt vection in the absence of any VIMS, none reported the opposite combination. Finally, we found that the simple act of making a button press leads to a detectable head movement even when using a chin rest. Taken together, our results indicate that the visual system is capable of predicting optic flow when self-initiated, to affect behaviour.

Key words: vection, ERP, ERD, postural sway, motion sickness, predictive coding.

INTRODUCTION

Sensory consequences of self-initiated actions

Self-initiated actions can have their own sensory consequences. These self-produced sensory stimuli need to be predicted, and compensated for, in order to allow both perceptual stability and efficient motor control (Von Helmholtz, 1867; von Holst and Mittelstaedt, 1950; Rao and Ballard, 1999). Navigating an environment, for example, evokes optic flow. Forward translational motion generates radially expanding visual flow (Diels and Howarth, 2013), an important contributor to perceptual processing of self-motion (Pitzalis et al., 2013). The physical properties of optic flow can be similar independently of whether an observer is actively moving through an environment, or is rather being moved passively (or even if the visible environment is moving, Durgin et al. (2005)). Yet it is important to discriminate between the different possible causes of any given visual flow as they may have different implications, in terms of the required response (Brooks and Cullen, 2019). Therefore, it is crucial to study how the brain deals with the consequences of active and passive self-motion through the environment to get a fuller understanding of normal navigation (Bansal et al., 2018). Active and passive self-motion have been studied

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Abbreviations: AR, augmented reality; ERD, event-related alpha desynchronization; ERP, event-related potential; VIMS, visual induced motion sickness; VR, virtual reality.

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0306-4522/

with various types of motion, whether in a car, plane, or on foot, in addition to operating motion simulators, or the use of augmented or virtual reality (AR and VR). For example, studies have compared active head turns with conditions where the participant is turned by external forces (Blouin et al., 1998), playing a driving console video game actively or watching the replay of the same race passively, as a passenger would (Dong et al., 2011), navigating a VR environment actively or viewing a recorded journey (Havranek et al., 2012; Riecke and Feuereissen, 2012), or comparing walking with passive horizontal displacement of the participant (Durgin et al., 2005). In the vestibular system, the sensory organs detecting head acceleration are stimulated independently of whether a head turn is actively generated or passively applied. Strikingly, at a very early stage of subcortical processing (the vestibular nuclei) the neuronal response in rhesus monkeys is suppressed when they actively move their head relative to their body (Brooks and Cullen, 2019; Cullen and Minor, 2002; Sadeghi et al., 2007; Jamali et al., 2009). There is also a modulated neuronal response downstream in cortical motion sensitive visual areas (dorsal part of medial superior temporal lobe, MSTd) even in stationary monkeys, if actively steering optic flow compared to passively viewing the same stimuli (Page and Duffy, 2007).

Visual stabilisation after head movement was discussed in early seminal work (von Holst and Mittelstaedt, 1950) and more recently it has been suggested that the related research field of the sense of agency can be extended to the control of virtual environments (Haggard, 2017). Self-initiated action outcomes evoke reduced cortical activity in visual and auditory cortices compared to the same stimuli presented unexpectedly (Straube et al., 2017). Whether observers were moving actively or passively influenced the perception of 3D visual spatial structure (Riecke and Feuereissen, 2012). Arguments have been put forward for both attenuation and enhancement of processing of self-initiated stimuli, and these may not be mutually exclusive (Press et al., 2020).

Optic flow effects: brain activity

Optic flow has several striking effects on the human brain, such as activations and deactivations in widespread brain regions such as the motion-sensitive visual areas (the human V5/MT + complex), parts of the posterior insular cortex (PIVC), and regions within the superior parietal lobe and the intra-parietal sulcus (e.g. putative human VIP). Areas VIP and MST + seem to be highly relevant for the processing of translational self-motion (Pitzalis et al., 2013). Alpha-band oscillations (8–13 Hz) correlate with synchronized rhythmic changes in the membrane potentials of neuron populations reflecting phases of high- and low excitability (Klimesch et al., 2007). High cortical alpha activity in a specific brain region is associated with selective inhibition of task-irrelevant processing (Klimesch et al., 2007; Jensen and Mazaheri, 2010) while changes in alpha are thought to be involved in processes such as expectancy and predictions (Harris, 2005) e.g. via phase re-alignments to achieve specific alpha phases which facilitate and ameliorate stimulus processing at the time of stimulus processing (Barry et al., 2004). Optic flow suppresses neural oscillations, as measured by event-related desynchronization (ERD (Ehinger et al., 2014; Palmisano et al., 2016; Vilhelmsen et al., 2015)) with similar effects to vestibular or kinaesthetic stimulation (Ehinger et al., 2014), and is associated with increased experience of presence in VR (Kober et al., 2012). Alpha-band ERD can be interpreted to reflect the end of the modulatory effect of alpha (Klimesch et al., 2007), or disinhibition (Edwards et al., 2018). It is unclear which neural processes are sensitive to whether optic flow is self-initiated or externally generated.

Optic flow effects: posture

Optic flow influences postural control and can make standing or sitting people sway (Lishman and Lee, 1973; Sparto et al., 2006; Palmisano et al., 2014; Fujimoto and Ashida, 2020), compensating for an erroneously expected momentum shift. Different aspects of postural control may be explored by either measuring the shift of weight across the feet (Winter et al., 1996) or by recording head- and body sway separately (Guerraz et al., 2001; Sparto et al., 2006; Dong et al., 2011; Pitzalis et al., 2013; Fujimoto and Ashida, 2020). Head-mounted accelerometers allow studying effects of any postural response on head movement during exposure to self-initiated or externally-generated optic flow. Any such head motion is important because this can itself generate additional sensory stimulation, via producing additional optic flow, or stimulating the vestibular organs.

Optic flow effects: subjective

Optic flow can induce two key subjective phenomena: firstly, vection, a highly compelling conscious experience of illusory self-motion, even in stationary observers e.g. (Palmisano et al., 2015; Berti and Keshavarz, 2020). Converging evidence indicates the importance of the influence of cognitive factors on vection perception (Kitazaki and Sato, 2003; Riecke et al., 2006; Riecke, 2010; Palmisano et al., 2015; D'Amour et al., 2021). The full scope of the functional significance of vection is still unclear (Palmisano et al., 2015). Secondly, visual induced motion sickness (VIMS) is triggered by various types of visual stimuli including the optic flow that can cause vection (Keshavarz et al., 2015). Typical symptoms include oculomotor disturbances like eye strain, blurred vision and headache combined with disorientation in the form of vertigo or dizziness, autonomous dysregulations like pallor, sweating and hypotension, gastrointestinal symptoms such as nausea, vomiting and stomach awareness, as well as diffuse arousal disturbances like drowsiness, fatigue and difficulty concentrating (Golding and Gresty, 2015; Bertolini and Straumann, 2016; Keshavarz et al., 2021). It is hard to predict what proportion of people will experience VIMS during experiments, as multiple factors affect prevalence, such as stimulus characteristics, experimental setting, and the equipment contribute to estimates diverging widely between 1% and 80% in laboratory settings (Keshavarz et al., 2021). While vection is generally

assumed to be a welcome experience in VR, VIMS needs to be reduced as much as possible to allow the highest user acceptance (Palmisano and Riecke, 2018; Keshavarz et al., 2021). The exact relationship between vection and VIMS is still a matter of debate (Webb and Griffin, 2002; Bonato et al., 2008; Ji et al., 2009; Diels and Howarth, 2011; Keshavarz et al., 2015; Nooij et al., 2017), with implications for the broad acceptance of VR and AR technologies in neurorehabilitation, education, research and entertainment (e.g. Berti and Keshavarz, 2020). VIMS is reduced when participants can control the start and end of their exposure to a rotating optokinetic drum (Levine et al., 2014).

Aims of the current study

We therefore devised the current experiment, in which we aimed to test whether self-initiation (versus passive onset) of otherwise identical optic flow stimuli would affect three distinct but potentially related consequences of optic flow: head motion, reported visual motion-related sensations (vection and VIMS intensity) and alpha desynchronization in the EEG.

In the substantial literature on self-initiation, stimulus initiation tends to be differentiated into distinct forms using variations of the terms "self", "other" and "computer-generated" (Weiss et al., 2011). For the purpose of our study, we use the terms ‘‘self-initiated” or ‘‘active” whenever the participant triggers either self-motion or visual self-motion cues actively by a motor action, here pressing a button. The condition in which the visual self-motion cues were computer-generated is called ‘‘externally-generated” or ‘‘passive”. In addition, we also looked at the methodological issues of the development of VIMS intensity during the course of the experiment and the effectiveness of using a chin rest in these types of neurophysiological studies.

We predicted that the sway would be stronger in the self-initiated condition compared to the passive condition and that it would be more time-locked to the stimulus onset, based on previous work showing that in a virtual driving video game, drivers swayed more than passengers (Dong et al., 2011). We expected the vection intensity to be lower when self-initiated based on the idea that self-initiation leads either to sensory attenuation as observed in other sensory modalities (Blakemore et al., 1998; Weiss et al., 2011; Stenner et al., 2014), or to other processes that are more related to general predictive mechanisms (Kaiser and Schütz-Bosbach, 2018). We included VIMS measurements: (1) to identify whether participants felt unwell and (2) to contribute to the growing literature explicitly comparing vection and VIMS (Keshavarz et al., 2015). We expected a bilateral posterolateral ERD in the alpha band evoked by optic flow (Ehinger et al., 2014; Vilhelmsen et al., 2015; Palmisano et al., 2016), reflecting cortical disinhibition (Edwards et al., 2018) during stimulus processing. Based on the concept of sensory attenuation of self-initiated stimuli, we expected weaker disinhibition (and therefore weaker ERD) in the self-initiated condition. Likewise, we expected a modulation of early negative deflections of the event-related potential (ERP) (Hughes and Waszak, 2011) induced by the optic flow onset. Finally, as usually implicitly assumed, we expected that sway would be inhibited by the usage of a chin rest.

EXPERIMENTAL PROCEDURES

Participants

Twenty-nine healthy right-handed adults (mean age: 25 ± 4 years, range: 21–32; 16 female) with no history of neurological or psychiatric illness and normal or corrected-to-normal vision participated in our study. Due to high levels of VIMS (pre-defined exclusion criterion: $\geq$15 on the fast motion sickness scale (FMS), from 0: ‘‘no sickness at all” to 20 ‘‘frank sickness” (Keshavarz and Hecht, 2011)), one participant was unable to participate in the full experiment, and so analysis is therefore restricted to their mean vection and peak sickness ratings. All subjects provided written and informed consent and were financially compensated. The protocol was approved by the local ethics committee.

Stimuli

The stimuli consisted of a movie with a globally coherent radially expanding optic flow pattern simulating straight forward translation towards the fixation cross presented with different expansion speeds. Before the beginning of each block, the expansion speeds were randomly assigned integers from the range 10 to 90. Each speed was equally likely, with 90 approximately 9 times as fast as 10. The movie was created using MATLAB (The MathWorks Inc., Natick, MA) using the PsychToolbox (PTB-3, v3.0.13) add-on. The pattern consisted of white dots on a black background with a white fixation cross in the centre. The movie was generated by first randomly positioning 12,000 white dots in 3D space. Their exact size and position were then calculated based on the perspective of the observer and correspondingly projected onto one movie frame. This was repeated for each frame while the observer virtually moved through 3D space. The individual frames were then converted into a movie. The stimuli were designed to recreate some of the most important basic features of real-life optic flow (acceleration towards the periphery of the visual field, object looming and motion parallax, etc). Briefly: the movie presentation consisted of two phases lasting one second each: first, the speed steadily increased to reach its maximum after one second. This speed was then maintained for an additional second in the second phase Afterwards the optic flow stopped, and the static frame was shown for another second. See https://osf.io/zm2vn or https://youtu.be/dPtBffNKqHY or Supplementary video 1 for an example. In more detail: each trial (see Fig. 1) consisted of a static frame presented for 1 s, followed by a colour change of the fixation cross as a cue signal to get ready which lasted 0.5–1.5 s. The following static frame was presented for 0.5–1.5 s in the passive condition, or until the participant pressed the button in the self-initiated and the button-press-only condition. On self-initiated or passive trials, optic flow was presented, consisting of

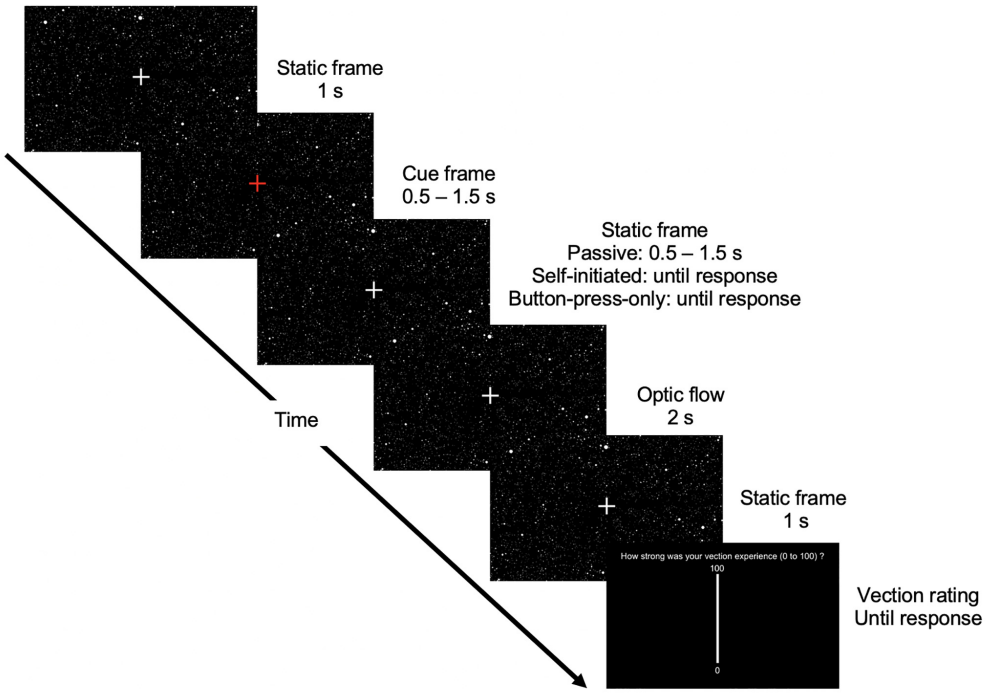

Fig. 1. Task schematic showing the three conditions. On self-initiated flow trials participants initiated flow onset by pressing a button. On passive flow the flow was started by the computer and they did not press a button. On button-press only trials they pressed a button but there was no optic flow.

1 s of accelerating optic flow followed by 1 s of continuous optic flow, followed by a third static frame presented for 1 s, and the vection rating display. By contrast in the button-press only condition, there was no optic flow, no static frame, and no vection rating display.

Experimental design

The overall design of our experiment into self-initiated (‘‘button press starts the optic flow”), passive (‘‘optic flow starts after a random time interval without pressing a button”) and motor-only control conditions (‘‘repeated button-presses without optic flow”) follows the classic design of studies of agency (Gentsch and Schütz-Bosbach, 2011). The use of random speeds by contrast allowed the dissociation of expectations about the timing of stimulus onset, which was only predictable and controllable in the self-initiated condition, and the speed/intensity of the stimulation, which was unpredictable in both the self-initiated and in the passive optic flow condition. Stimuli were projected onto a screen (2.0 m × 1.5 m) with an eye-to-screen distance of 1.15 m using an Epson EB-425 short throw projector (refresh rate 60 Hz) and a mirror, to increase visual angle of projection (see Fig. 1).

Participants sat on a rotatable bar stool behind a chin rest with their feet on a footrest attached to the chair. The height of the stool was adjusted so that the fixation cross was in the centre of their field of view (Fig. 2). To prevent additional cues regarding (lack of) self-motion, participants were seated so that their backs did not touch the backrest. They wore custom-made glasses with peripheral occluders which reduced their field of view to 90 × 60 degrees of visual angle preventing them from being able to see beyond the edges of the screen. Various optic flow stimuli have been used before: we designed the stimuli in a way that their timing was predictable in the active condition while their intensity (velocity) was random and could not therefore be anticipated; this led to a dissociation of intensity prediction and temporal prediction, isolating possible effects of temporal attention (Miniussi et al., 1999; Doherty et al., 2005; Correa et al., 2006). We employed a manual button press for initiating flow, to parallel previous work on sensory attenuation of self-initiated auditory stimuli (Gentsch and Schütz-Bosbach, 2011; Bansal et al., 2018). Responses were made using a standard computer mouse which rested on their right thigh during all conditions. All participants responded with their right index finger.

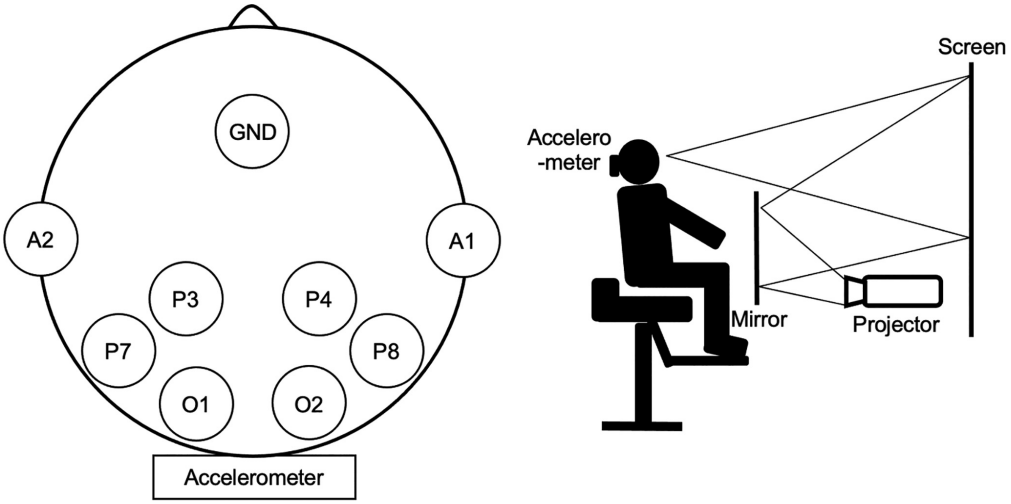

Fig. 2. Montage of EEG electrodes and the accelerometer (left) and participants' posture relative to the screen (right). The eye-screen distance was 1.15 m and the visual angle 90° × 60°.

The main experiment was preceded by five practice self-initiated and five practice passive trials. The main experiment as a whole consisted of three different conditions: self-initiated flow in which button-press starts optic flow immediately, passive flow in which optic flow starts after a random time interval without pressing a button, and a button-press-only control condition in which participants performed button-presses without optic flow. The experiment comprised 8 blocks of self-initiated flow and 8 blocks of passive flow with 20 trials per block, leading to a total of 160 self-initiated flow and 160 passive flow trials, as well as control blocks before and after the main experiment, in which participants performed a fixation block and a button-press-only block, taking 3 min each. Half of the blocks within each condition were performed using a chin rest and half without (counterbalanced order); this design allowed us to analyse visual induced postural responses (VIPR) in sitting participants (on the blocks without chin rest, so that participants could sway freely) as well as ERPs/ERDs (on the blocks with chin rest, to reduce movement artefacts). The mean number of trials ± standard deviation performed within the 3 min button-press-only condition per participant was similar (67.0 ± 9.7 without chin rest and 66.4 ± 9.6 with chin rest).

Subjective reports

Participants were asked to rate their vection experience after each trial on a vertical visual analogue scale (VAS) from 0 (''No vection") to 100 (''I felt like I was really moving"). They submitted their ratings by pressing the left mouse button after moving the cursor to the point on the VAS where it described their experience best. The term 'vection' was defined clearly on an information sheet to allow comparability between vection studies (Berti and Keshavarz, 2020) as: *"the experience that you are moving when you are not really. You may have experienced it before, for example during the "train illusion". This may happen sometimes if you are sitting in a still train at a station, and the train next to you starts to move, sometimes causing the illusory feeling that you are moving".* At the end of each block, participants verbally reported their VIMS level using the fast motion sickness scale (FMS, Keshavarz and Hecht, 2011) on a scale from 0 (''no sickness at all") to 20 (''frank sickness").

Electroencephalogram (EEG)/accelerometer

Data was recorded with Brain Vision Recorder Professional software (V. 1.21.0303) and was amplified using a LiveAmp amplifier (Brain Products, Munich, Germany) held in a custom-made pocket on the back of the EEG cap. This lightweight system used 6 Ag/AgCl electrodes (BrainCap, Brain Products, Munich, Germany) placed according to the 10/20 system (O1, O2, P3, P4, P7 and P8). EEG was referenced to the right earlobe and re-referenced offline to the average of both earlobes using the MATLAB toolbox EEGLAB (v13.5.4b) (Delorme and Makeig, 2004). The ground electrode was at Fz and an electrooculogram electrode was placed below the right eye (vEOG). Impedance for all channels was kept $\leq$10 kΩ and the signal was sampled with a rate of 1000 Hz. The amplifier's built-in accelerometer therefore measured a combination of head- and body accelerations along three orthogonal axes relative to the earth's gravitational acceleration in the units: $mg = 9.81 * 10^{-3} \frac{m}{s^2}$.

Data pre-processing

Data pre-processing, analysis and statistics were performed in MATLAB using the EEGLAB (v13.5.4b) and the 'Statistics and Machine learning' toolboxes. Only chin rest blocks were considered in the EEG analysis while only blocks without chin rest were considered for the accelerometer analysis (i.e. visual-induced postural response, VIPR) except for the comparison of overall sway with- and without chin rest. This design minimized the introduction of noise into our EEG data from potential movement artifacts and avoided problems with multiple comparisons in the sway data which would arise from the comparison with and without chin rest for all dependent variables. Trials were epoched relative to optic flow onset, with the preceding 200 milliseconds used for baseline correction by subtraction of the mean of the signal during the baseline from EEG signal during the trial (Cohen, 2014). For EEG analysis, trials with an amplitude range exceeding $>100\ \mu V$ (EOG) and $>120\ \mu V$ (in any other channel) during baseline and the time of interest were rejected. These values were based on visual inspection of the raw data. EEG data was low- (<40 Hz) and high-pass filtered (>0.3 Hz, Probst et al., 1993). The accelerometer as it lay in the cap was slightly tilted away from true vertical and horizontal axis. To recover acceleration in true vertical and horizontal co-ordinates we derived the magnitude of the true forward-/backward acceleration vector from the raw measured forward-/backward acceleration:

$$|acceleration_{y,z}(t)| = \sqrt{acceleration_z(t)^2 + acceleration_y(t)^2}$$

To recover directional information from the acceleration data, we multiplied the magnitude of the acceleration vector with the normalized $acceleration_z$.

$$acceleration_{virtual}(t) = \frac{|acceleration_{y,z}(t)| * acceleration_z(t)}{|acceleration_z(t)|}$$

Trials were rejected if signal range during the baseline exceeded >40 mg or if peak amplitude during the whole 2 s of the trial exceeded $+/-$ 50 mg. To avoid projecting the button-press into the trial, we used -500 to -301 ms before optic flow onset for baseline correction again by the mean method (Cohen, 2014) in VIPRs. Data on self-initiated and passive trials were epoched to optic flow onset. To allow direct comparison with the button-press only condition (in which there was no optic flow) we calculated the time it took for the computer to trigger the optic flow after button press in the self-initiated condition, which was 50 ms (three frames of 16.6 ms each). The time-point 50 ms after button press was then used as time zero in the button-press condition.

Data analysis and statistical testing

For the analysis, we used either non-parametric (Wilcoxon Signed Rank) tests or parametric tests (*t*-test where appropriate given the normality and equality of variances of the data as determined by the Lilliefors Test *lilietest()* and Levene's Test *vartestn()* with test type 'LeveneAbsolute', variables were treated as random effects). The ERPs were formed as the grand average from epochs lasting up until 500 ms after the optic flow onset. Time-frequency EEG analysis used the complex Morlet wavelet convolution based on the fast Fourier transformation (for a description see Cohen, 2014) with a frequency window of 4 Hz–20 Hz (individual frequencies were calculated as 30 logarithmically spaced frequencies in this frequency window with 4 Hz being the first and 20 Hz being the last frequency). Epochs lasted from 3.5 s before to 3.5 s after optic flow onset, to avoid edge artifacts (Cohen, 2014). Time-frequency plots show the decibel-scaled change of power during the optic flow compared to pre-trial baseline (decibel conversion as described by Cohen, 2014). We derived the alpha-band-specific power change as the mean power change for each timepoint between 8.7 Hz and 12.8 Hz. The accelerometer data was analysed in a similar fashion to the VEPs to form grand averaged visual induced postural responses (VIPRs) taken from epochs lasting until 1000 ms after optic flow onset.

RESULTS

Behavioural results

The mean vection rating was 35.0 ± 3.9 out of 100 on the VAS. There was no significant difference between vection ratings on self-initiated compared to passive trials ($t_{27} = -0.98$, $p \geq 0.05$) nor between FMS ratings after self-initiated and passive blocks (mean active: 1.53, mean passive: 1.63, $Z = -0.83$, $p \geq 0.05$). A paired-sample two-tailed t-test showed that vection experience was rated higher without a chin rest compared to with one (36.7 ± 4.0 vs. 33.4 ± 3.9, $t_{27} = 3.78$, $p \leq 0.001$). Median vection magnitude and peak sickness ratings were positively correlated across individuals (Fig. 3, $\rho = 0.58$, $p < .001$). Visual inspection of Fig. 3 also shows an additional pattern, whereby there are participants who perceive strong vection with zero VIMS (data points clustered on the y-axis), while there was no participant who reported VIMS without any vection. Participants used a wide range of values for vection ratings, consistent with previous reports that vection varies over time, and that participants engaged with the rating task (Kuiper et al., 2019).

Accelerometer results

We looked at the overall sway defined as the sum of the absolute sway over the whole time when optic flow was present (0–2000 ms after start of optic flow). Fig. 4 shows the corresponding visual evoked postural response. Overall sway was significantly reduced by the usage of a chin rest (1126.0 mg vs. 626.7 mg, $Z = -4.01$, $p \leq 0.0001$). We then tested within the blocks without a chin rest whether there is any effect of agency on sway. As Fig. 5 shows, the main difference we identified was the forward-then-backward sway at around the start of optic flow. This difference was present on self-initiated flow trials and button-press-only, indicating that it represents the sway elicited by the button press. To further analyse this, we isolated the forward acceleration component and compared the peak

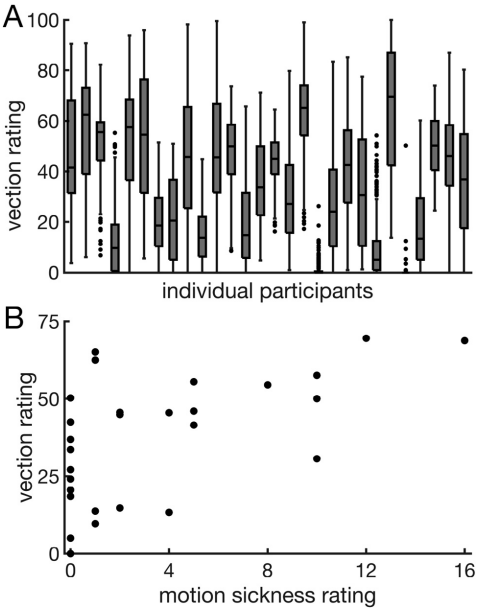

Fig. 3. (A) Vection rating for each individual participant and the variability over the course of the experiment. Horizontal lines inside boxes show median of vection ratings. Boxes show interquartile range. Whiskers show the highest and lowest non-outlier rating (quartiles defined as 0.75 respective 0.25 quartiles). **(B)** Vection and Visually Induced Motion Sickness correlated. Each dot represents one participant. Additionally, vection could occur in the absence of sickness, but not vice versa.

sway across conditions (Fig. 6). Peak sway was significantly higher in active compared to passive flow ($Z = 2.64$, $p \leq 0.01$). Interestingly, it was even higher in the button-press-only condition compared to active ($Z = -2.32$, $p \leq 0.05$; button-press-only vs. passive: $Z = 3.87$, $p < .0001$): most sway occurred on trials without flow but with a button press; with less sway on self-initiated flow; and the least on passively initiated flow.

Event-related potentials

A large negative deflection starting at around 130 ms and lasting until around 170 ms was present on self-initiated compared to passive or button-press-only conditions (note that ERPs to long-lasting moving stimuli look different from VEPs time-locked to a short, flashing stimulus (Heinrich, 2007), e.g. we did not expect to see the VEP components evoked classically by static flashed stimuli such as P300). This time window of interest (130–170 ms) is in line with previous EEG studies of vection (Berti et al., 2019). We performed paired-sample two-tailed t-tests where appropriate and Wilcoxon Signed Rank tests where normality and/or equality of variances were violated to compare the amplitude of the negative deflection in the different agency conditions (self-initiated vs. passive, self-initiated vs. button-press-only and passive vs. button-press-only for each EEG channel) with a Bonferroni-corrected $\alpha = 0.0028$ ($\alpha = 0.05/18 = 0.0028$). ERP amplitude was significantly higher in self-initiated compared to passive trials at channels O2 ($Z = -3.19$, $p \leq 0.001$, $t = -2.05$), P3 ($Z = -3.10$, $p \leq 0.01$) and P4 ($Z = -3.35$, $p \leq 0.001$). Marginally significant effects in channel O1 ($Z = -2.82$, $p \leq 0.01$), P7 ($Z = -2.35$, $p \leq 0.05$) and P8 ($Z = -2.12$, $p \leq 0.05$) did not survive multiple comparison correction. To check whether the effect can be accounted for by the button press, we compared self-initiated flow and button-press-only trials in the same time window. The amplitude of the deflection was significantly higher in active flow for channels P3 ($t_{27} = -4.11$, $p \leq 0.001$), P4 ($t_{27} = -4.67$, $p \leq 0.0001$) and P8 ($t_{27} = -3.56$, $p \leq 0.01$) and marginally significant for channels O1 ($t_{27} = -2.59$, $p \leq 0.05$), O2 ($t_{27} = -3.22$, $p \leq 0.01$) and P7 ($t_{27} = -2.48$, $p \leq 0.05$). To find out whether the deflection is also present in passive flow, we compared passive flow and button-press-only. There was no significant difference in any channel present (all p's > 0.27).

Event-related desynchronization

We looked at the power change relative to baseline across conditions (self-initiated vs. passive, self-initiated vs. button-press-only, passive vs. button-press-only for each EEG channel) and across hemispheres within conditions (O1 vs. O2, P3 vs. P4 and P7 vs. P8 each in the active and the passive condition) using paired-sample two-tailed t-tests where appropriate and Wilcoxon Signed Rank tests where normality and/or equality of variances were violated. To address multiple comparison issues, we used a Bonferroni-corrected $\alpha = 0.0021$ ($\alpha = 0.05/24 = 0.0021$). There was a significant alpha ERD in all channels in self-initiated and passive flow conditions compared to the button-press-only condition (all p's < 0.0001). As hypothesized, ERD was stronger on passive compared to self-initiated flow, specifically at left parietal channel P7 ($t_{27} = 3.52$, $p \leq 0.01$). Based on prior findings on the lateralization of spatial functions, we also compared the ERDs within conditions between hemispheres (O1 vs. O2, P3 vs. P4 and P7 vs. P8). ERD overall was stronger in each and every right hemisphere electrode than its left hemisphere counterpart, when self-initiated (O1 vs. O2: $Z = 3.35$, $p \leq 0.001$; P3 vs. P4: $Z = 4.26$, $p < .0001$; P7 vs. P8: $t_{27} = 0.47$, $p < .001$) unlike in the passive condition (O1 vs. O2: $Z = 0.25$, $p \geq 0.80$; P3 vs. P4: $Z = 1.30$, $p \geq 0.19$; P7 vs. P8: $Z = 2.05$, $p \geq 0.04$).

Control analyses

An additional analysis, motivated by the sway results, was performed to help rule out whether the differences in ERPs between self-initiated and passive trials were attributable to button pressing being only present on self-initiated trials. If so, such an ERP modulation would be expected in the button-press only condition. Fig. 7 shows the positive deflection before optic flow onset on self-initiated and button-press-only conditions,

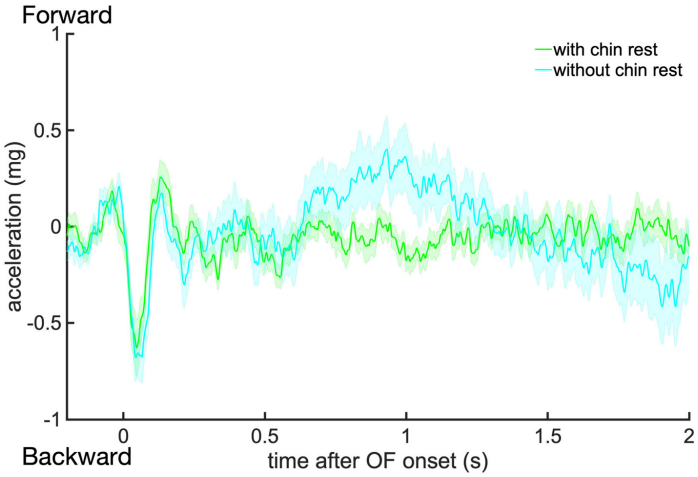

Fig. 4. Three sway responses were distinguishable in the data with a chinrest (green) compared to without a chin rest (blue). Shaded error bars represent standard error of the mean. The first short forward–backward component at around 0 ms reflects the sway induced by the button-press. The second component is a forward acceleration starting at around 500 ms after optic flow onset and the third, more pronounced sway, reflects a backward acceleration starting at around 1.3 s after optic flow onset. The latter two components are effectively inhibited by the chinrest while the first component was independent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

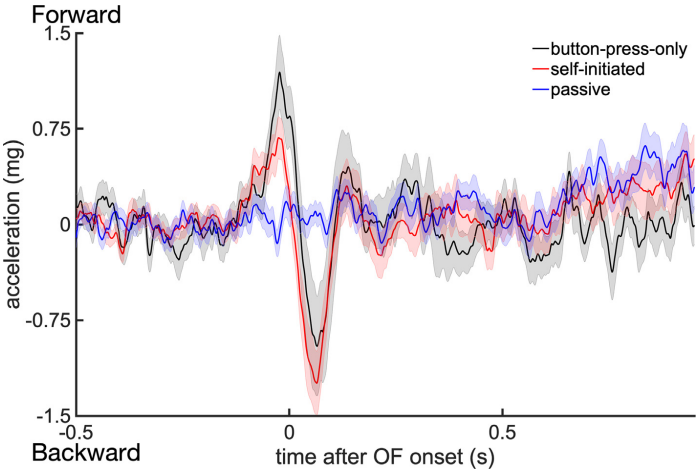

Fig. 5. Visually induced postural sway responses differed on self-initiated (red), passive (blue) and button-press-only (grey) trials. Shaded area represents the standard error of the mean. The first forward–backward acceleration component at around the time of optic flow onset is not present in the passive condition and is weaker in self-initiated compared to button-press-only. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

presumably reflecting a signal related to the button press. Importantly however, there was no deflection in the ERP during the button-press-only condition at the time of the prominent negative deflection in the other conditions (see ERP results, above). Button-pressing could also not explain the differences between ERD on self-initiated versus passive trials. Visual inspection of the power spectra (see Fig. 8) confirmed by one-sampled two-sided Wilcoxon tests for all channels showed that there was no significant change in alpha power in the button-press-only condition compared to baseline (all p's $>$ 0.19). Therefore, the EEG effect (the difference between active and passive trials) cannot be attributed to the motor response (or head motion, see above) of button pressing. We also directly compared the EOG data on self-initiated and passive trials. There were no significant differences in eye movements during the negative deflection (130–170 ms after optic flow onset: $Z = -0.32$, $p \geq 0.75$). As an additional control, we checked whether people's heads were moving differently at the time of the negative deflection (130 ms–170 m s). A paired-sample Wilcoxon Signed Rank test showed no significant difference between sway in self-initiated and passive trials ($Z = 0.73$, $p \geq 0.47$).

In an exploratory analysis, we found a marginally significant finding namely that participants did press the button faster on self-initiated trials (mean = 0.84 s, range: 0.30 s–1.77 s) trials compared to the random delay on passive trials (mean = 1.00 s, range: 0.93 s −1.09 s) trials ($Z = 1.89$, p = .06). Although this did not pass the threshold for significance, we wanted to rule out the possibility that any differences between the ERPs on self-initiated versus passive trials could be due to such differential reaction times. We therefore analysed the ERPs for channel P3 and P4 with only the half of participants showing the slowest RTs (only participants with RT $\geq$ 0.75 s included) to start self-initiated trials (15/28 participants removed, Fig. 9). This did not eliminate the effect (P3: $t_{27} = -4.35$, $p < .05$; P4: $t_{27} = -3.69$,

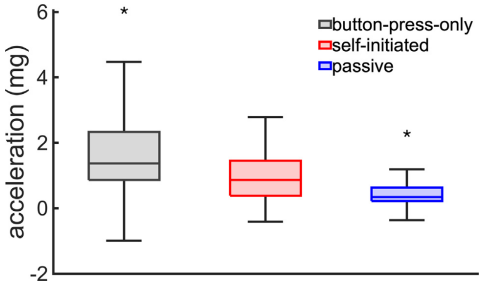

Fig. 6. Forward sway in the first component. Between −35 ms before and 5 ms after optic flow onset for the three conditions button-press-only (grey), self-initiated (red) and passive (blue). The horizontal line in the box plot shows the median, the box marks the interquartile range and the whiskers show the highest and lowest non-outlier values. Asterisks show outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

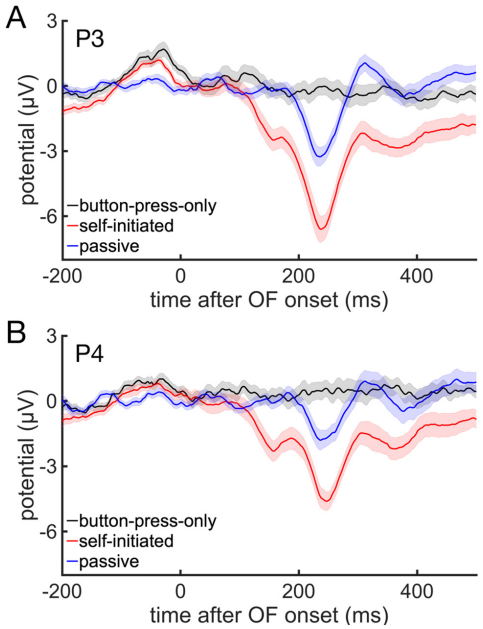

Fig. 7. ERP for self-initiated flow (red), passive flow (blue) and button-press-only (grey) for the left (P3, upper, **(A)**) and right (P4, lower, **(B)**) parietal channels. Shaded area around the ERPs represents the standard error of the mean. A prominent negative deflection between 130–170 ms was observed in the self-initiated condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$p \leq 0.01$), indicating independence of cue related influences, also indicating a highly consistent effect across participants.

DISCUSSION

Summary

We examined whether self-initiation modulated the effects that optic flow has on behaviour and brain activity. As discussed below, self-initiation inhibited the ERD in the alpha band over the left hemisphere, increased the amplitude of a negative deflection between 130 and 170 ms after flow onset, and stabilized postural sway. We additionally found that button-pressing itself caused a postural sway. We also report a positive correlation between vection ratings and reported VIMS and suggest a differentiation into two susceptibility groups.

Event-related alpha power

Optic flow led to a large ERD across all channels, in line with previous optic flow studies (Ehinger et al., 2014; Vilhelmsen et al., 2015; Palmisano et al., 2016). Consistent with sensory attenuation, the ERD was weaker in the self-initiated condition: a weaker alpha desynchronization, meaning increased alpha power, indicates inhibition of neural processing (Harris, 2005; Herrmann et al., 2016; Edwards et al., 2018). While cortical alpha is thought to reflect inhibition of task irrelevant brain regions (Jensen and Mazaheri, 2010) with the function of preventing interference (Klimesch et al., 2007), ERD can be thought of as disinhibition (Edwards et al., 2018) of stimulus processing. The difference between alpha-power in self-initiated versus passive trials may reflect processes occurring on self-initiated or on passive conditions. "Prospective feelings of non-agency" (Haggard and Chambon, 2012) may have led to a stronger ERD on passive trials. Alternatively, sensory suppression via self-specific (Blakemore et al., 1998; Blakemore et al., 1999a; Blakemore et al., 1999b; Bansal et al., 2018) or general predictive mechanisms (Hughes et al., 2013; Stenner et al., 2014; Kaiser and Schütz-Bosbach, 2018) may have led to a weaker ERD on self-initiated trials, for example if additional information about the stimulus timing allows some processing before the actual stimulus onset (Correa et al., 2006), requiring less resource deployment, producing less ERD.

Event-related potentials

ERPs showed a large negative deflection on self-initiated trials. Previous work has also found increased ERP deflections in an action-to-effect condition broadly equivalent to our self-initiation condition (Hughes and Waszak, 2011). Temporal attention also affects modulation of visual ERP components (Doherty et al., 2005; Correa et al., 2006) and one key aspect of self-initiation likely to drive the current findings is that when participants themselves initiated the flow, they knew when it would come (Correa et al., 2006). Effects of temporal attention seem to be most evident in tasks with a high perceptual demand (Correa et al., 2006), and the combination of our complex radially expanding acceleration stimuli with a high number of dots, with the perceptual judgements of a very subjective experience, may have led to precisely such a high task demand. The negative ERP deflection

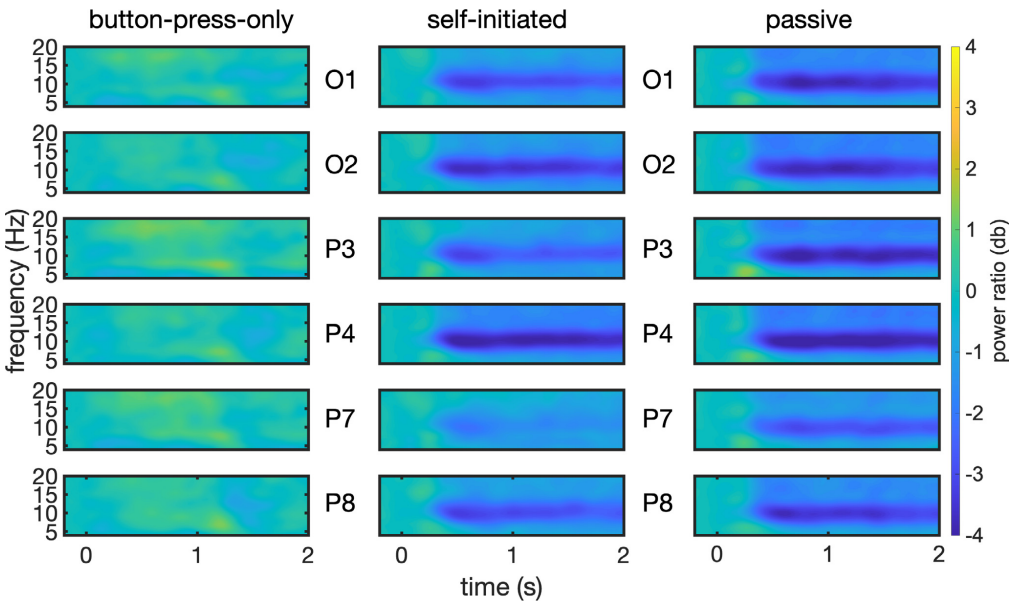

Fig. 8. Power spectra (db-scaled power ratios) relative to optic flow onset in the button-press-only (left column), self-initiated (middle column) and passive condition (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric parieto-occipital channels. The colour bar on the right shows the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Optic flow evokes event related desynchronization in the alpha band (blue) If the flow onset was self-initiated, this ERD was inhibited, prominent at left parietal electrode P7, corrected for multiple comparisons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

may reflect general predictive mechanisms in the visual system, mediated by the directing of visual attention. Future work may test the putative account that an early parietal deflection is the source of the direction of processing resources with the later ERD reflecting the site of this attention modulation: for example, recent work showed that dorsal parietal TMS affected the normal ERP modulation during a visual-vestibular task (Willacker et al., 2019).

Postural responses

At the end of the acceleration phase of the stimulus (Fig. 4), 1 s after optic flow onset in the no chin rest condition, we observed a head acceleration in the direction of the perceived forward vection, consistent with previous research for sitting participants (Fujimoto and Ashida, 2020). The peak of this average postural response across subjects (not associated with the button-press) was approximately one second after stimulus onset, i.e. the time when the acceleration stopped and the optic flow switched to linear movement for one second. Although the rate of acceleration was unpredictable, the time of the acceleration stopping was predictable, and this postural response could be accounted for as a reaction to this change. Later on, during the constant velocity phase, the sway pattern reversed (Fig. 4) and this backward acceleration peaked towards the end of the trial (Fujimoto and Ashida, 2020). This pattern has been interpreted as acting to reduce the sensory conflict which is thought to elicit motion sickness, by generating corresponding vestibular input (Keshavarz et al., 2015).

Postural data showed that participants' heads moved even on trials where they were using a chin rest and that this was strongest on the control trials without optic flow in which participants simply pressed a button, presumably reflecting postural compensation for a change in balance caused by the act of button pressing. In our study we had participants sit in a particular fashion, on a stool without leaning back, to minimize somatosensory input that might disrupt vection. Future work can test whether this is specific to this postural response or reflects a response potentially generalizable to a large variety of experimental and applied situations. This first sway component, at around the time of the button press, was not present in the passive flow condition and can therefore not be attributed to the optic flow per se. The sway induced by the button press was present but significantly reduced (i.e. stabilized) in the self-initiated flow condition. Future work can examine whether this intermediate postural stabilization response reflects the anticipation of visual flow speed onset, and which may not only stabilize posture in response to visual motion cues but also to the sway induced by

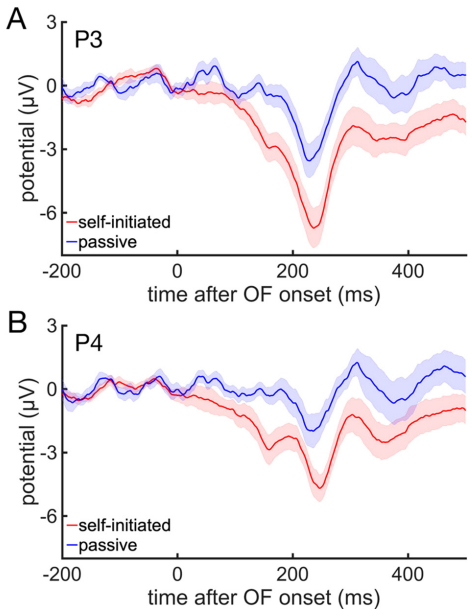

Fig. 9. ERPs after removal of participants with short reaction times for self-initiated (red) and passive (blue) trials for the left (P3, upper, **(A)**) and right (P4, lower, **(B)**), parietal channels after removal of all participants with a median reaction time between cue-offset and button-press of < 750 ms (N = 13). Shaded area around the ERPs represents the standard error of the mean. The prominent negative deflection at around 130–170 ms is still observable in the self-initiated condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pressing a button. By contrast, the later sway component was effectively reduced by the use of a chin rest and is likely to reflect a postural reaction to the optic flow. This component of sway was not affected by self-initiation (Winter et al., 1996; Guerraz et al., 2001) which may be because participants were sitting: sitting is thought to elicit different swaying patterns (Fujimoto and Ashida, 2020), and prevents the usage of the full arsenal of postural control (e.g. the ankle method, Winter et al., 1996), the cortical involvement in which grows with increasing postural task difficulty (Edwards et al., 2018).

Vection eliciting capacity of our stimuli

We used short exposure times to optic flow to facilitate looking at ERPs elicited by the optic flow onset (see Methods for example movie). This contrasts with previous studies using long epochs in which vection did not normally start right away but needed time to build up (Riecke and Feuereissen, 2012). There is a substantial range in the literature, with reported vection onset latencies starting from at least 1 to 2 s (Berthoz et al., 1975; Warren, 1995), mostly 1 to 10 s (Dichgans and Brandt, 1978; Palmisano et al., 2015; Palmisano and Riecke, 2018), although latencies from 2 to 30 s (Riecke et al., 2006; Riecke and Feuereissen, 2012) or even from 0.46 to 40 s have been reported (Seno et al., 2017; Seno et al., 2018). Additionally, our optic flow stimuli use a velocity profile which accelerates smoothly from zero, and not a large sudden step-change of motion onset: this is not usually used in vection studies but which we found to be particularly striking during task development. On the one hand, the visual-vestibular conflict theory of vection (Zacharias and Young, 1981) would assume that accelerating stimuli are not going to induce vection, because they elicit a stronger conflict which inhibits the sensation of self-motion. On the other hand, recent work (Palmisano et al., 2008; Palmisano et al., 2011; Palmisano and Riecke, 2018) suggests that the addition of jitter and oscillations to optic flow (in the form of random or periodic accelerations along different axes relative to the direction of perceived continuous self-motion) led to shorter vection onset latencies and often also higher intensities. The account proposed was that the more complex global visual motion patterns lead to increased allocation of processing resources towards the visual information compared to pure continuous optic flow. Another reason for why participants may have experienced vection with such short epochs could be that participants' exposure to global motion might have sensitized them to the experience of vection in the subsequent trials as previously suggested (Palmisano and Riecke, 2018) based on prior observations (Ito, 2004). Indeed in this experiment participants were repeatedly exposed on every trial to radially expanding optic flow without any intermittent static trials, or other directions of flow. Examining this would again require a different design, for example to rule out confounds from practice effects leading to higher vection ratings. Vection ratings overall were on average 35 out of 100, and longer epochs may evoke stronger vection, albeit with the concomitant cost of longer experiments, or fewer trials. Ultimately future separate experiments will be necessary to compare (at least) the potential roles of acceleration, flow direction, sensitisation, practice, trial intermixing, and epoch length.

Relationship of vection and visually-induced motion sickness

The relationship between vection and visually-induced motion sickness has long been a matter of debate (Keshavarz et al., 2015). While vection is a welcome user experience in many VR applications (Keshavarz et al., 2019), users reject technology that makes them experience symptoms such as nausea, headache, blurred vision, arterial hypotension, etc. (Golding and Gresty, 2015; Keshavarz et al., 2015; Bertolini and Straumann, 2016). Consequently, these recent technological developments have led to a surge in interest in the role of the visual system in the genesis of VIMS and motion sickness in general. Traditional motion sickness is exacerbated when people cannot see the road ahead (Turner and Griffin, 1999; Turner, 1999) potentially attributable to a reduced capacity for predicting motion consequences in the absence of the optic flow. Note however that VIMS and traditional motion sickness differ insofar as physical motion is often small or even absent in the first while

being more important in the latter (Keshavarz et al., 2015).

No participant in the current study experienced VIMS without any vection, which is in line with the literature suggesting that vection is a prerequisite for VIMS (Hettinger et al., 1990; Smart et al., 2002; Diels and Howarth, 2011; Keshavarz et al., 2015). There have however been reports of VIMS-like symptoms in the absence of vection (Ji et al., 2009), with stimuli designed for each participant individually in such a way that vection was suppressed (based on work by Brandt et al., 1973); a possible explanation (Keshavarz et al., 2015) raises the question of whether the observed symptoms are really related to self-motion eliciting VIMS or to other aspects of the stimuli.

We furthermore found a positive correlation between vection magnitude and motion sickness intensity, as has been reported earlier by some (e.g. Bonato et al., 2008; Diels and Howarth, 2011; Keshavarz and Berti, 2014) but not others (e.g. Ji et al., 2009; Keshavarz et al., 2019; Webb and Griffin, 2002). It has been suggested that vection magnitude may be less important than the interaction between scene- and self-motion (Nooij et al., 2017), or the change in vection intensity (Bonato et al., 2008). This latter account can potentially explain why our experiment did often induce substantial motion sickness despite using blocks and trials shorter than used in many previous studies e.g. (Hettinger et al., 1990; Smart et al., 2002; Webb and Griffin, 2002). In addition, we note that visual inspection reveals two subgroups of participants. The one group perceived the full spectrum of vection magnitudes but with zero or almost zero VIMS, the second group showing the strong positive linear correlation. This could be another possible explanation for why there are contradictory results concerning the correlation of vection and VIMS, especially for studies testing fewer participants than in the current study (of 29).

LIMITATIONS & FUTURE WORK

Self-initiation only reduced ERD on left hemispheric channels. Furthermore, the ERD over the left hemisphere was only smaller than over the right hemisphere in the self-initiation condition, with no such lateralization in the passive condition. Although left hemisphere parietal cortex has been associated with the perception of self-generated movements (e.g. Sirigu et al., 1999), the low spatial resolution of EEG, including the current study which used a mobile head-mounted EEG system with a relatively low number of channels, precludes inferring spatial localization of neural signals. Additionally, in the current study participants always responded with their contralateral right hand. Future studies using more EEG channels, other methods, and bimanual responses, may elucidate further the spatial location of this effect.

Our stimuli are highly abstract in comparison to more naturalistic VR setups – such as a virtual simplified road (Vilhelmsen et al., 2015) or a virtual rollercoaster task (Riccelli et al., 2017) – which in turn may come with their own limitations such as potential variance from distraction by other stimuli. All types of purely visual optic flow necessarily lack the multisensory (proprioceptive, somatosensory, vestibular, auditory, etc) feedback during real-life locomotion (Fajen, 2021). Additionally in our experiment participants initiated flow with a button press, clearly less ecologically valid than for example a head movement or walking (notwithstanding the use of buttons for acceleration in racing cars, gaming etc), but with far fewer risks of producing EEG artefacts from motion due to comprising a single brief movement of an effector some way away from the head. Recent mobile EEG developments offer a rich potential to overcome previous technical problems with recording EEG during locomotion (Ehinger et al., 2014; Dowsett et al., 2020). It would be interesting to compare the consequences of self-generated optic flow after button pressing with that occurring for example after head turning or locomotion. This could test, for example, whether the consequences of self-initiated actions are particularly strongly suppressed (e.g. at earlier levels) if the effector moved (unlike the right index finger) is already part of a vestibular reflex loop. Effects of compensation for movement at very early central levels are sensitive to whether or not the head is moved with or relative to the trunk, and so whether vestibular stimulation is accompanied by proprioceptive (Roy and Cullen, 2001; Roy and Cullen, 2002).

Our stimuli lack the ‘bob and sway’ oscillations that would be present in walking subjects (Palmisano et al., 2008; Palmisano et al., 2011; Palmisano and Riecke, 2018); our stimuli resemble more the visual environment in a train, car or wheelchair, than walking.

Our self-initiated condition was not designed to determine whether the effects of the manipulation of control over the optic flow manipulation are caused by self-specific or general predictive mechanisms (Kaiser and Schütz-Bosbach, 2018). Future studies will be needed to clarify the relative importance of the acting self in the context of the attenuation of self-produced signals.

Vection intensity was rated at the end of each trial while VIMS was only rated at the end of the block. It would be interesting to compare the co-occurrence of both phenomena over time with the resolution of individual trials, although that bears the risk of tiring participants further. Similarly, here button-press-only blocks were presented only before and after the experiment. Future work intermixing flow trials with others trials could also test for possible effects of sensitization across trials (Palmisano and Riecke, 2018), and in its interaction with VIMS because of the striking potential for making use of the ‘‘vection advantage” in applied settings (Riecke et al., 2012; Palmisano et al., 2015).

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroscience.2021.07.003.

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6. Experiment 3

Self-initiation Inhibits the Postural and Electrophysiological Responses to Optic Flow and Button Pressing.

6.1 Introduction

This chapter contains additional data which was not presented in the paper (Obereisenbuchner, Dowsett et al. 2021). The main focus here lies on the neurophysiological correlates of vection and the effects of optic flow speed on the ERD and the VEP. Based on the literature (see introduction to Experiment 2) and our own previous results, we expected to observe a significantly stronger ERD during faster compared to slower than average trials which might also mediate the ERD during high and low vection trials. In line with previous studies, we proposed to find an effect of optic flow speed on the N2 amplitude (Maruyama, Kaneoke et al. 2002, Heinrich 2007, Vilhelmsen, van der Weel et al. 2015), even though we did not observe this effect in Experiment 2.

6.2 Methods

The methods are presented in the paper (Obereisenbuchner, Dowsett et al. 2021) and the general methods section of this thesis.

6.3 Results

Event-related potentials

In addition to the analysis of the effect of the agency condition on the VEP which was already presented in the paper (Figure 36 shows the ERPs for the additional channels which were only reported as text), we also compared the event-related potentials in trials with different vection intensities (Figure 37) and for different speeds (Figure 38). Paired-sample two-tailed t-tests if appropriate given the assumptions of normality and equality of variances, or Wilcoxon Signed Rank tests if the assumptions were violated, were used to compare the amplitude of the ERPs around the negative deflection N2 (see Chapter 1) in the time interval 200 to 300 ms after optic flow onset. While there was again no significant difference for the comparison of high and low vection trials (all $p > .05$), we found an increase in the amplitude with higher speeds for channels O1 ($t_{27} = -2.53$, $p \leq .05$), P3 ($t_{27} = -4.03$, $p \leq .001$), P4 ($Z = -2.94$, $p \leq .01$) and P7 ($t_{27} = -3.83$, $p \leq .001$). There was a marginally significant difference for Channel O2 ($t_{27} = -$

2.53, p = .088) but no significant difference for P8 (t_{27} = -1.27, p > .05). In a next step, we compared the amplitude of the VEPs across hemispheres with data from all conditions pooled; and indeed, we found the amplitude to be significantly higher for all left hemispheric channels compared to their right hemispheric counterparts (O1 vs. O2: t_{27} = -4.74, p ≤ .0001; P3 vs. P4: t_{27} = 6.79, p ≤ .000001; P7 vs. P8: t_{27} = -5.86, p ≤ .00001).

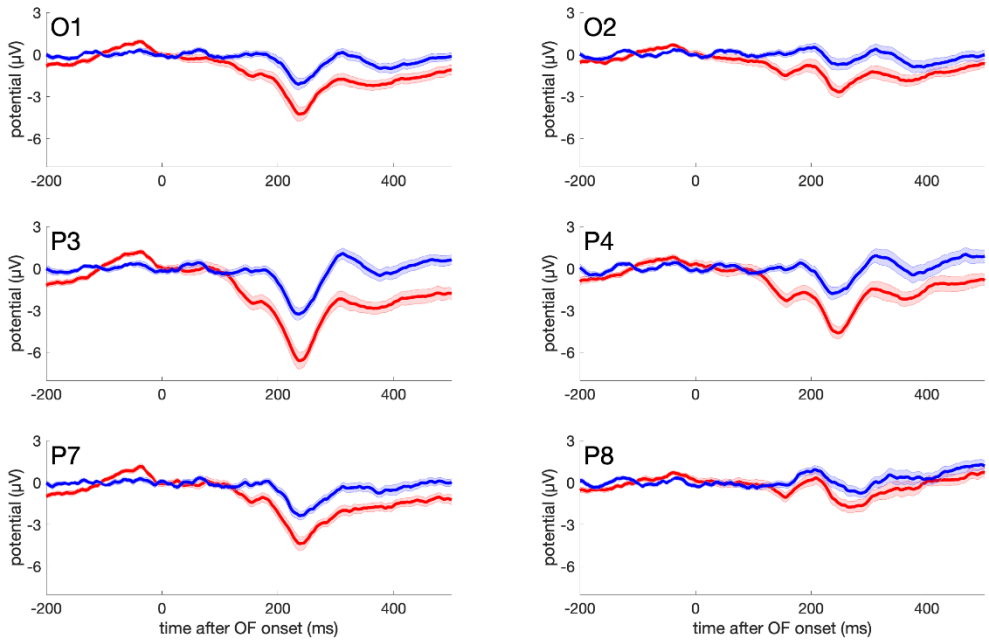

Figure 36: ERP for self-initiated flow (red) and passive flow (blue) for all parietal and occipital channels. Shaded area around the ERPs represents the standard error of the mean. A prominent negative deflection between 130–170 ms was observed in the self-initiated condition. This figure includes the ERP for P3 and P4, which were already published in the paper (Obereisenbuchner, Dowsett et al. 2021).

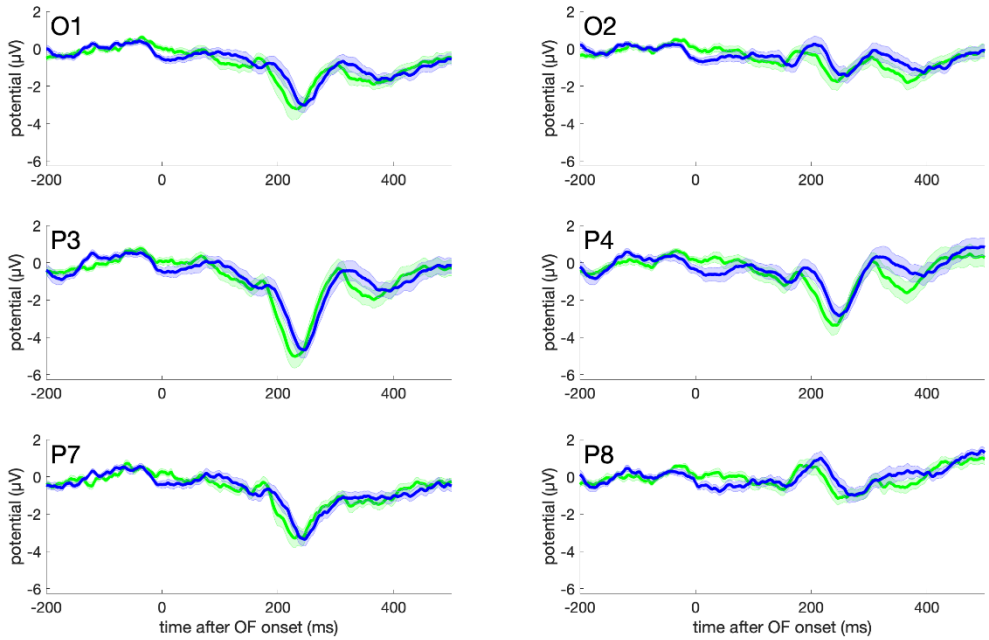

Figure 37: ERP for trials in which participants rated their vection experience to be high (green) and low (blue) for all parietal and occipital channels. Shaded area around the ERPs represents the standard error of the mean. The N2 component in the interval 200-300 ms is the most prominent feature.

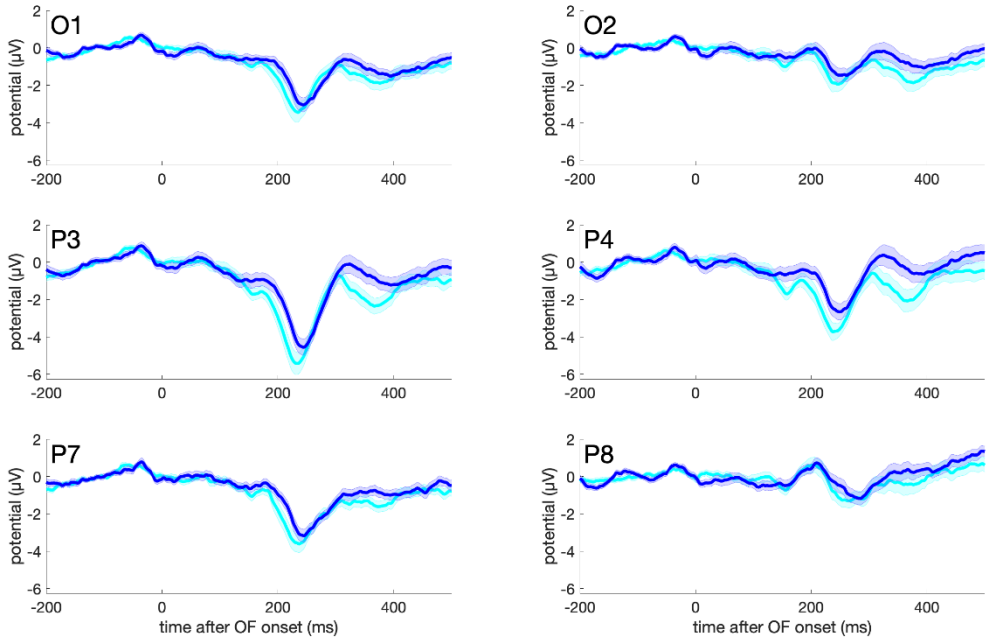

Figure 38: ERP for faster than average (light blue) and slower than average trials (dark blue) for all parietal and occipital channels. Shaded area around the ERPs represents the standard error of the mean. The N2 component in the interval 200-300 ms is the most prominent feature. Note that the amplitude seems to be higher in the ERP of fast trials.

Event-related desynchronization

We tried to reproduce the findings from Experiment 2 by using the same analyses in the same time windows, with the same filter settings and wavelet configuration with the spectral data from sitting participants. Contrary to Experiment 2, there was no significant difference between the ERD for high and low vection trials (Figure 39, all $p > .05$). The only significant finding was a stronger ERD during fast compared to slow trials (Figure 40) for channel P4 ($Z = 2.03$, $p \leq .05$).

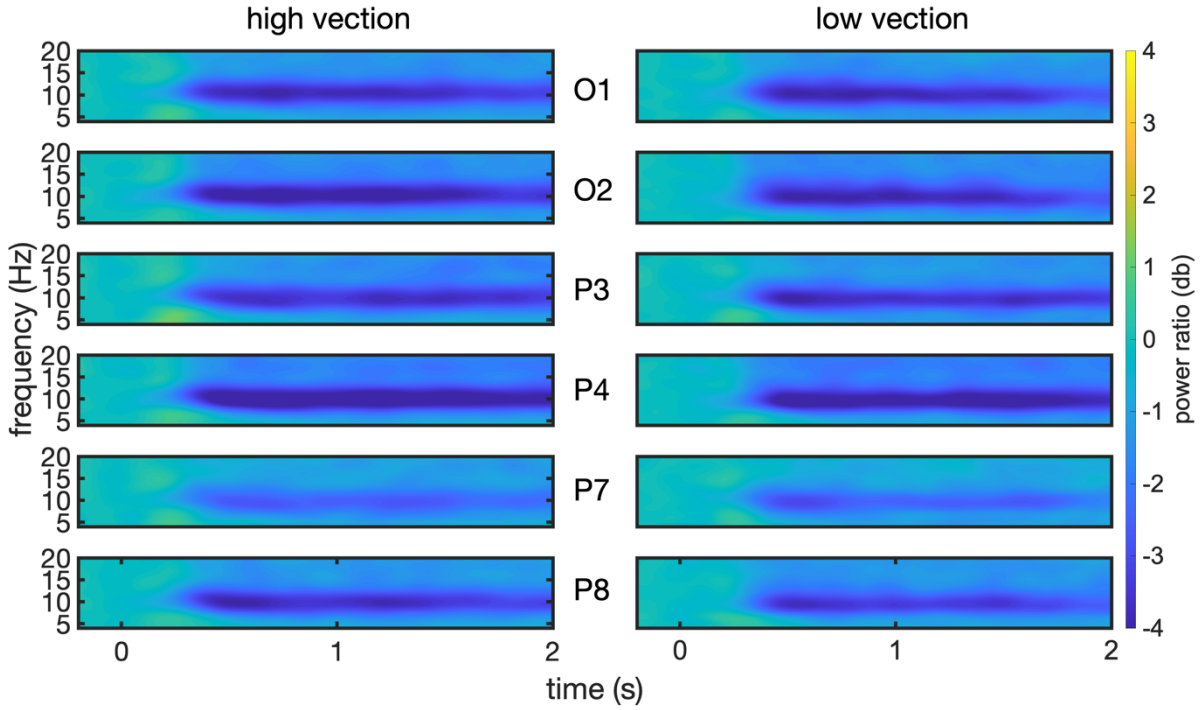

Figure 39: Power spectra (db-scaled power ratios) relative to optic flow onset in trials in which participants rated their vection experience to be high (left column) and low (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric. The colours encode the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Event related desynchronization in the alpha band (blue) is evoked by optic flow which seems to be almost identical in both conditions.

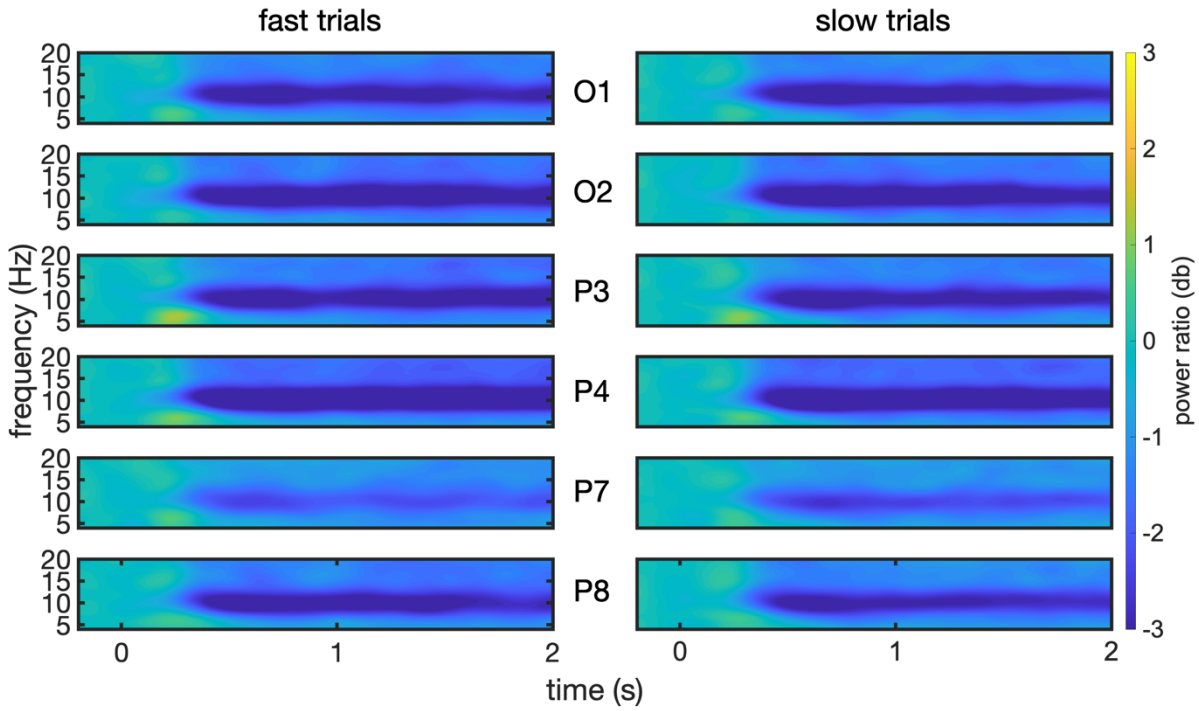

Figure 40: Power spectra (db-scaled power ratios) relative to optic flow onset in faster than (left column) and slower than average trials (right column) for all channels. O1, P3 and P7 are left hemispheric and O2, P4, P8 are right hemispheric. The colours encode the db-scaled power change relative to the mean power of the baseline period (the 200 ms before optic flow onset). Event related desynchronization in the alpha band (blue) is evoked by optic flow which seems to be almost identical in both conditions except for channel P4, where statistical analysis showed a significantly stronger ERD during fast trials.

6.4 Discussion

For the discussion of the findings already published, please see the paper. This section thus focuses on the unpublished results. The main additional analysis was the comparison of the amplitude of the N2 component in the VEP for different speeds. In line with prior findings, we observed an increase in the amplitude in faster trials; this deflection is thought to include signals from e.g. MT with possible contributions from V3 / V3A (see Heinrich for a review (Heinrich 2007)). As previously observed, the N2 amplitude might show a lateralization in motion-onset VEP studies (Andreassi and Juszczak 1982, Göpfert, Schlykowa et al. 1988, Kubová, Kuba et al. 1990, Kuba and Kubová 1992, Hollants-Gilhuijs, De Munck et al. 2000), while most PET studies show bilateral activation without any indicators of lateralization (Zeki, Watson et al. 1991, Watson, Myers et al. 1993, Cheng, Fujita et al. 1995). Hollants-Gilhuijs et al. argue that this might be due to averaging of the activity data which obscures individual hemispheric dominance (Hollants-Gilhuijs, De Munck et al. 2000). Indeed, different studies

have shown that individuals within the study population might exhibit different lateralization of the VEP; Kubová et al. for example observed in a study of 80 participants that ~60% showed right-sided and 20% left-sided lateralization (Kubová, Kuba et al. 1990). Importantly, their findings were independent of handedness. Tootell et al. showed that human area MT in the dominant hemisphere gets input from both hemifields in contrast to earlier visual areas (Tootell, Reppas et al. 1995). Hollants-Gilhuijs et al. confirmed this observation and described a lateralization with a source on the right side in 4/6 and a left-sided source in 2/6 of their subjects (Hollants-Gilhuijs, De Munck et al. 2000). Andreassi and Juszczak found a lateralization only in female participants (Andreassi and Juszczak 1982) which was, however, to the best of our knowledge not reproduced in another study. Despite the high inter-individual variability which might be responsible for the conflicting results, it seems as if lateralization might be an important feature of visual motion processing; the physiological reason for the increased amplitude in one hemisphere might be the combined input from the ipsi - and contralateral hemifield.

6.5 Comparison of the results of the different experiments

We compared the participants' median vection ratings across the different experiments using independent-sample two-tailed t-tests. Vection ratings were significantly higher in Experiment 1 compared to Experiment 3 ($t_{36} = 2.54$, $p \leq .05$) and marginally significantly higher in Experiment 1 compared to Experiment 2 ($t_{27} = 1.78$, $p = .086$). There was no significant difference between the vection ratings in Experiment 2 and 3 ($t_{45} = 1.02$, $p > .05$). Because of the strong lateralization of the N2 amplitude in Experiment 3 (all left hemispheric channels significantly stronger than their right sided counterparts), we checked whether the lateralization was also present in Experiment 2. Interestingly, this effect could not be observed in Experiment 2 (all $p > .05$, P3 vs. P4: $t_{18} = 1.98$, $p = .06$). Quantitative comparisons of the absolute values of the EEG potentials are of limited relevance; a more qualitative approach is therefore applied in the general discussion.

7. General Discussion & Limitations

7.1 Experimental design

Considering our experimental design, especially in the light of our neurophysiological measurements and the lateralized response in Experiment 3, it needs to be pointed out that participants responded and started the optic flow using their right index finger with the mouse being placed on their right thigh. It would be interesting to repeat our study with the mouse in the left hand or using a counterbalanced design, to completely rule out any disturbances, even though the button-press-only control condition and our analyses present strong evidence that our main findings cannot be explained by the button-press and are even very robust (see in the paper). If one assumes that the button press or the somatosensory stimulations from the mouse placement are responsible for the lateralized agency response, it should be present in Experiment 2 as well as in Experiment 3. As this was not the case, other underlying factors seem much more likely (see the discussion of the neurophysiological findings).

One aspect which complicates studying active and passive navigation and makes it harder to compare different studies, is the vast number of possible designs; given the increasing evidence that linear and circular optic flow lead to dissociable patterns of brain activation, this needs to be taken into consideration before generalizing the findings from other studies as well as the ones from our own experiments. As already mentioned in the introduction of the paper, examples for those study designs are active head turns compared with passive head rotations by external forces (Blouin, Labrousse et al. 1998), matched-control driving simulator video games with one group actively playing the game and the other group watching the replay (Dong, Yoshida et al. 2011) or similar ideas with navigating virtual environments (Havranek, Langer et al. 2012, Riecke and Feuereissen 2012) or walking contrasted with passive horizontal displacement (Durgin, Gigone et al. 2005). Generally, those studies use either monosensory stimulation or a combination of different senses such as vision, vestibular, proprioception and more or less complicated mechanisms of active control such as button presses versus walking. Different types of navigating our environment include but are not limited to walking, cycling, active and passive transportation as in a car, boat, bus, plane or train or as mentioned before, the same types of navigation but in more or less convincing virtual scenarios. Those forms of navigation produce e.g. dif-

ferent types of optic flow, as the often studied vertical ‘bob and sway’ oscillations produced by walking (Palmisano, Allison et al. 2008, Palmisano, Kim et al. 2011, Palmisano and Riecke 2018) while pure forward translation simulating stimuli such as ours are more common in e.g. public transportation. While it comes with some disadvantages for transferability to study navigation in highly abstract settings such as in a dark laboratory room, wearing unfamiliar glasses and an EEG cap while being asked to rate subjective phenomena is indisputably very different from navigation in real life, but it still offers the unique opportunity to isolate the sensory qualities that one wants to study; in real life, the sensory content perceived during navigation, has an additional unpredictable component like independently moving objects or acting agents which might easily re-direct attention and “contaminate” behaviour, postural responses and brain activity. While it is often automatically assumed that more natural VR environments are ‘better’, there might just as well be a fine line beyond which the environment resembles the real environment so much that small differences or distortions might feel even stranger than our abstract stimuli, similar to the so called ‘Uncanny valley’ (Mori, MacDorman et al. 2012). A possible way to make use of the advantages of different methods would be to combine mobile EEG setups as e.g. developed by Dowsett et al. (Dowsett, Dieterich et al. 2020) with controllable, abstract environments containing features from real environments such as the virtual road from Vilhelmsen et al. (Vilhelmsen, van der Weel et al. 2015) or the simulated city from Maguire et al. with real navigation e.g. in a large room using head mounted displays (Maguire, Burgess et al. 1998).

Concerning the contributions of our work to the sense of agency field, it must be noted that we explicitly did not disentangle whether self-specific or general predictive mechanisms (Kaiser and Schütz-Bosbach 2018) are responsible for the neurophysiological and postural modulations found in Experiment 2 and 3. Additionally, it is not clear yet, what the functional significance of those findings is and whether another study design might be able to show their correlates on the behavioural level; we did not find an effect on vection intensity (which is discussed below in more detail), on visual induced motion sickness magnitude, on the precision of speed estimates or on the perceived speed in general. Durgin et al. in contrast observed a reduction in the perceived speed when participants walked actively on a treadmill (Durgin, Gigone et al. 2005). This was however also the case when participants were passively displaced in the direction of simulated self-motion. It can therefore be assumed that studies which found alterations in

perceived speed might be better explained by the integration of the information as provided by other sensory modalities (e.g. biomechanical simulation of walking forward). Reduced speed estimations in those cases cannot be attributed to sensory attenuation in the traditional sense because they are neither related to self-specific nor to general-predictive mechanisms (Kaiser and Schütz-Bosbach 2018) but rather to conflicting sensory information which is normally presented in a concordant way and only experimentally dissociated. Another possible reason for the absence of an agency effect in our studies is that participants were not able to predict the optic flow completely just because they caused it with their button-press: the onset timing was controlled by them, but the maximum speed and velocity profile were both unpredictable in either condition. Another reason for why we might not have been able to show differences in e.g. their speed estimation errors was that humans are generally very good in estimating optic flow speed, at least as long as they are provided with some scaling information (Frenz and Lappe 2005, Festl, Recktenwald et al. 2012); this scaling information might be cues like familiar objects placed in the virtual environment (Festl, Recktenwald et al. 2012) which provide size cues or reference speeds as long as they can assume that the environment stays the same (Bremmer and Lappe 1999, Frenz and Lappe 2005). In fact, participants might just be too good in estimating optic flow speed and the task design might lead to additional relocation of attentional resources which might cancel out all agency effects.

The absence of differences in VIMS ratings following self-initiated and passive blocks of approximately 3 min duration might be due to the markedly longer VIMS onset latency in the order of 10-15 minutes (Diels and Howarth 2011); the blocks might just have been too short to demonstrate a clear effect.

7.2 Across all modalities

One possible explanation for the absence of clear neurophysiological or postural signatures of vection is that while the sorting of trials with a higher and lower than median vection rating is a valid way to separate the trials into high and low vection groups, the median vection ratings in Experiment 2 and 3 were below 50 and one could argue that the two groups' vection experiences may not differ enough to see clear behavioural, postural or neurophysiological differences. Most studies using a similar rating scale reached slightly higher vection intensities (Riecke and Feuereissen 2012, Kuiper, Bos et al. 2019, Fujimoto and Ashida 2020) however as pointed out by Berti and Keshavarz,

the comparison of vection magnitude between different studies needs to be interpreted carefully (Berti and Keshavarz 2020). Albeit the absence of behavioural and postural effects and the absence of a clear neurophysiological effect, unambiguously attributable to vection (not a combination of vection and speed) must not indicate the inexistence of such. The dilemma with the type of experimental design we used is that while longer trials might elicit stronger vection sensations, the coupling of action (the button press) and effect (the optic flow) might wane over time and could also eliminate sensory modulation if it exists on a behavioural level for vection. Therefore, our trial duration and the resulting lower but consistently elicited vection can be seen as a trade-off between different factors. For further discussion of vection experience in our studies see the paper and the discussion of the behavioural results.

7.3 Behavioural level

As expected (Palmisano, Allison et al. 2015), there were high inter-individual differences in median vection ratings across all experiments. Interestingly, the vection intensity seems to drop over the course of the three experiments. One might argue that this can be seen as evidence against the acceleration advantage of vection (Palmisano, Allison et al. 2008, Palmisano, Kim et al. 2011, Guterman, Allison et al. 2012, Palmisano and Riecke 2018) and for the visual-vestibular conflict theory (Zacharias and Young 1981); it must however be noted that the optic flow in Experiment 1 was not only moving with a continuous speed but also 2.5 times longer (5 s). Given the fact that many studies use longer exposure durations (e.g. to make sure that vection is reliably induced, the mere existence of a vection experience after only 2 s, while also reported in other studies (Berthoz, Pavard et al. 1975, Dichgans and Brandt 1978, Warren 1995, Seno, Sawai et al. 2017, Palmisano and Riecke 2018, Seno, Murata et al. 2018), can be seen as evidence for an acceleration advantage or at least the absence of an acceleration disadvantage as postulated by the visual-vestibular conflict theory. As already discussed in the paper, another factor explaining the vection experience of our participants might be a sensitization effect due to the repetitious exposure to global motion, in our case with only short breaks in between and no changes in direction of optic flow, as proposed by Palmisano and Riecke (Palmisano and Riecke 2018) based on work by Ito (Ito 2004). However, to meaningfully discuss those theories, one would need to vary the optic flow duration and e.g. the number of

trials without a break individually, ideally in a study design not based on vection magnitude but rather on the onset timing as in Palmisano and Riecke's study (Palmisano and Riecke 2018). While Guterman et al. described higher vection in sitting participants (Guterman, Allison et al. 2012), our results are in line with Fujimoto and Ashida (Fujimoto and Ashida 2020), finding no significant differences between the varying postures.

Our study reproduced a classical finding that optic flow speed and vection intensity are highly positively associated, at least up to a certain optimal velocity (Brandt, Dichgans et al. 1973, Dichgans and Brandt 1978, Allison, Howard et al. 1999, Riecke 2010). One could point out that participants might not really rate their vection intensity but rather only the speed or a mixture of both with a strong bias by the speed differences. We therefore included speed estimations in Experiment 2. We assumed that asking for both experiences explicitly should implicitly emphasize that the two questions are distinct, and the rating needs to be based on different aspects of motion perception. It allowed us further to analyse the correlations for the shown optic flow speed with the speed estimations and the vection ratings. Our results demonstrate a high correlation for both comparisons, but they also show different distributions of the individual correlation coefficients with sometimes even negative correlations between vection and speed (see Figure 23) which suggests that participants indeed rated vection and speed separately. A potential study design which could contribute to the topic might use different levels of global coherence to modify the vection eliciting capacity of the stimuli without impairing speed judgements.

We observed no modulation of vection experience on the behavioural level attributable to active control. This was, as already expounded in the hypothesis section and the introduction, not utterly surprising, given the ambiguous previous results as pointed out by e.g. Riecke and Feuereissen (Riecke and Feuereissen 2012). Taking into account how logical it would be that such an effect exists given our current understanding of the human motor control system, it might however still be worth addressing in future studies, maybe by the usage of different methods to alter participants' implicit sense of control (Synofzik, Vosgerau et al. 2008, Gentsch and Schütz-Bosbach 2011, Haggard and Chambon 2012, Haggard 2017).

A point which was only superficially touched in the discussion of Experiment 2, is the interpretation of the VAS vection ratings. The decision to use the anchors 0 and 100 on the opposing ends of the VAS might encourage interpreting the vection ratings given

by the participants as percent values with 0 being no vection at all and 100 being full vection. This interpretation in turn might prompt the conclusion that our vection ratings were not full vection with different magnitudes but rather early conscious components of full vection caught in the process of building up (Riecke and Feuereissen 2012). The problem with differentiating the two respective interpretations is closely related to remarks by Palmisano et al., who pointed out that part of the problem is the ambiguous, imprecise definition of the whole concept of vection which is even more true for subconcepts such as vection intensity or the transition period between full object motion perception and preceding full self-motion perception (Palmisano, Allison et al. 2015). In those transition phases, participants will have to apply their own subjective definition which is based on their personal interpretation of the definition of vection on our participant information sheet. This contributes to the general ambiguity already inherent to the study of subjective phenomena underlining the need for objective markers (Keshavarz, Campos et al. 2015, Palmisano, Allison et al. 2015). It is therefore hard to dissociate the two interpretations from a theoretical standpoint alone. What might help, is an approach allowing for phenomenological variability. For someone who has already experienced striking vection, it is quite clear that there are different forms and intensities of an experience which is qualitatively very different from object motion. So one can assume that every participant who has experienced vection at least once, which is indeed what the informal debriefing brought to light, will probably use the VAS for relative intensity judgements. A potential problem with our study is that we cannot be 100% sure that each participant perceived striking vection at least once early enough during the experiment to make sure that the experience was rated as intended. This limitation can be overcome in future work e.g. by using an approach as described by Palmisano and Riecke (Palmisano and Riecke 2018) based on the method for magnitude estimation by Stevens (Stevens 1957). They used a standard stimulus, made sure that participants experienced vection, and then used this intensity as a reference for subsequent intensity ratings.

The vection eliciting capacity of our stimuli in epochs of 2 seconds was discussed in detail in the paper. Some other interesting aspects concerning the visuo-vestibular interaction are discussed here. According to the visuo-vestibular conflict theory by Zacharias and Young, vection onset latency is the time needed to resolve the sensory conflict elicited by the conflicting information following visual self-motion cues while the vestibular system signals stationarity (Zacharias and Young 1981). In recent years,

this theory has repeatedly been challenged in studies which have shown that the addition of accelerating components to the optic flow which should prevent the resolution of the conflict according to the predictions of the sensory conflict theory, actually increased vection intensity and reduced vection onset latency (Palmisano, Allison et al. 2008, Palmisano, Kim et al. 2011, Guterman, Allison et al. 2012, Palmisano and Riecke 2018). An alternative explanation proposed by Palmisano and Riecke (Palmisano and Riecke 2018) based on earlier work (Keshavarz and Berti 2014, Palmisano, Barry et al. 2016), it is rather the default visual processing which needs to be suppressed before vection can begin to build up. The effect of acceleration is then attributed to the increased allocation of processing resources following the exposure to the higher complexity of the global visual motion pattern. Additionally, the proposed sensitization of vection following recurrent exposures to global visual field motion in the same direction (Palmisano and Riecke 2018), based on observations by Ito (Ito 2004), fits quite well to the alternative explanation: the visual system stays primed to the type of stimulus and does not fully reach the state of default visual processing which consequently leads to vection starting to build up earlier. A possible extension of this suggestion is based on the observed visual-vestibular co-activation following exposure to accelerating visual stimuli (Nishiike, Nakagawa et al. 2002, Palmisano, Allison et al. 2015): the sensory conflict is resolved so rapidly because the visual system overrules the vestibular system via visual-vestibular co-activation. This could be either via the allocation of processing resources or by alterations in the default activity in a multisensory motion sensitive region which needs to be suppressed in addition to the visual activity (Keshavarz and Berti 2014, Palmisano, Barry et al. 2016). Future studies using functional imaging or electrophysiological methods with a good spatial and sufficient temporal resolution might be able to further elucidate the nature of the visuo-vestibular co-activation. The postulated sensitization of vection seems to be a promising line of research as well.

7.4 Neurophysiological data

A general limitation of our studies was the limited information on the neuroanatomical sources behind our findings. The low number of channels in itself confines the possibility to draw inferences and is further amplified by the widespread effects with findings frequently spanning more or even all recorded channels. The advantage of this setup was however that we could perform more hypothesis-driven analyses over channels

which have commonly been implicated in visual motion perception studies, with a faster and easier preparation and fewer problems with multiple comparison. We therefore accepted the limited spatial resolution in our experiments to study the interaction of vection, optic flow and self-initiation in general and inspire future studies which might address the anatomical source for e.g. the widespread, large negative deflection in more detail.

One of the main findings of our experiments was the reduced ERD in the alpha band during self-initiated exposure to optic flow compared to passive exposure to the same stimuli. Alpha activity is modulated during sensory stimulation and is thought to reflect memory and attentional processes (Herrmann, Strüber et al. 2016) via its two supposedly main mechanisms: inhibition of task-irrelevant information and coordination of timing of the cortical processing, which presumably are a fundamental basis for cognitive functions (Klimesch, Sauseng et al. 2007, Jensen and Mazaheri 2010, Herrmann, Strüber et al. 2016). Exposure to optic flow leads to a widespread alpha desynchronization over the parieto-occipital cortex (Ehinger, Fischer et al. 2014, Vilhelmsen, van der Weel et al. 2015, Palmisano, Barry et al. 2016) which can be interpreted as increased activity due to those areas being involved in processing (Harris 2005, Herrmann, Strüber et al. 2016, Edwards, Guven et al. 2018). The ERD duration seems to be closely linked to the time for which the stimulus stays relevant for the respective task (Kaufman, Schwartz et al. 1990) and modulations of alpha power are associated with vestibular processing and self-motion estimates (Dowsett, Herrmann et al. 2020). The fact that the ERD is reduced, corresponding to a reduced dis-inhibition in the self-initiated condition, is in line with sensory attenuation on the physiological level. In other words: as internal predictions, expectancy and motor preparations are reflected via changes in cortical alpha activity (Harris 2005), changes in pre-stimulus alpha are thought to be involved in preparing for upcoming events and their sensory feedback (Jensen and Mazaheri 2010). Klimesch et al. took this one step further and suggested that it is not the ERD which bares functional significance for stimulus processing but rather the temporally well-orchestrated end of the inhibitory alpha activity represented by the ERD (Klimesch, Sauseng et al. 2007). On the level of individual neurons, this corresponds to rhythmic changes in the membrane potentials, reflecting phases of higher - and lower excitability (Klimesch, Sauseng et al. 2007); a well-timed phase shift following predictions of the stimulus onset timing can influence the processing of stimuli

with essentially the same physical properties. This might be reflected by the more widespread sensory attenuation in response to self-initiation during the trial. A curious finding is the observation that the lateralized response in Experiment 3, with sensory attenuation only present in left hemispheric channels, was non-lateralized and present all over the parieto-occipital cortex in Experiment 2. Although we highlighted the association of the left-sided parietal cortex with the perception of self-generated movements (Sirigu, Daprati et al. 1999) in the paper, the distinct results require further discussion: the most obvious difference between Experiments 2 and 3 are the changes in posture during the exposure to optic flow. Therefore, the reason for the apparently inconsistent results might be variable weighting of the information provided by different sensory modalities in response to the increasing demands of postural stabilization during standing; this claim is supported by findings of Edwards et al., who described a reduction in (centro-parietal) alpha power with increasing task demands, thereby demonstrating that an influence of neurophysiological responses is per se possible (Edwards, Guven et al. 2018). Palmisano et al. suggested that accelerating optic flow leads to a visuo-vestibular co-activation which should be reflected in increased activity of bilateral visual cortices symmetrically and right-accentuated vestibular cortical areas (Palmisano, Kim et al. 2011). This could explain our findings in Experiment 3 as well as in Experiment 2 if one follows the proposition of different sensory weighting: the combination of large field visual stimulation with more complex postural stabilization might recruit more processing resources before motion onset following the assertion that not only the physical properties of the stimuli are important but also the neurophysiological properties of the system receiving them. A similar line of argumentation might also apply to the observed differences of the ERD during high and low vection as well as during fast compared to slow optic flow trials in Experiment 2. The fact that the speed effect was more widespread and more consistent, suggests that the differences in the neurophysiological responses to high - and low vection were indeed mediated by the high correlation of vection and speed rather than different vection levels. Furthermore, those alterations were only observable in Experiment 2, not in Experiment 3 and can neither be explained by differences in the median vection ratings (which were not significantly different between Experiment 2 and 3) nor by the speed as the stimuli used were identical. The most likely explanation is that it were the varying postural demands which altered the neurophysiological responses to the same stimuli.

For the interpretation of our findings, it is furthermore important to elucidate the relationship between ERDs and ERPs. Pfurtscheller and Lopes da Silva assume that the ERDs represent modulations of the activity of local interactions of main neurons and interneurons to control ongoing oscillatory activity while ERPs reflect the responses of clusters of cortical neurons to changes in afferent information, with a main difference being that ERPs are phase locked while ERDs are non-phase locked (Pfurtscheller and Lopes da Silva 1999). ERPs are thought to stem from the reorganization of the phases of ongoing cortical activity (Pfurtscheller and Lopes da Silva 1999) while brain oscillations are part of the mechanisms responsible for aligning the firing of neurons in a way which helps their signal superposition after the end of ongoing inhibition via alpha to prepare the regions involved in the processing for incoming signals, as inspired by Klimesch et al. (Klimesch, Sauseng et al. 2007). And in fact, pre-stimulus alpha phase can influence the amplitude and latency of the resulting stimuli and regularly appearing stimuli (i.e., expected stimuli) lead to phase adjustments towards more preferred states for processing (Barry, Rushby et al. 2004, Klimesch, Sauseng et al. 2007). And indeed, different components of the VEP have been associated with attentional processes and top-down modification (Doherty, Rao et al. 2005, Correa, Lupiáñez et al. 2006, Gentsch and Schütz-Bosbach 2011). As already proposed in the paper, we assume that the negative deflection at around 130-170 ms after optic flow onset might be the neurophysiological correlate of general predictive mechanisms which are only present in the self-initiated condition because of the phase locked nature of the ERP; even though there might be some predictions going on in the passive condition in which participants are also well aware that the optic flow is going to start soon, those predictions are however not time-locked as in the self-initiated condition in which participants know the exact timing of motion onset and would therefore be cancelled out during the calculation of the ERP. In line with the conceptualization of sensory attenuation (Bansal, Ford et al. 2018), Berti and Keshavarz proposed that the modulation of early visual ERP components to optic flow stimuli might reflect a sensory feedback loop which is an important foundation for the conscious experience of self-motion (Berti and Keshavarz 2020). An effect of self-specific or general predictive mechanisms on these components, as supported by our findings, would therefore fit well to the theoretical conceptualizations for both, the neurophysiological correlates of vection and sense of agency.

We found no differences in the VEP amplitudes of the second part of the negative deflection in the time interval 200-300 ms after optic flow onset for high - and low vection trials in either experiment. We assume that this component corresponds to the traditional N2 (Heinrich 2007, Vilhelmsen, van der Weel et al. 2015), explained in more depth in Chapter 1. In Experiment 3 however, we found an increase in the N2 amplitude in faster trials which is in line with prior findings by most (Maruyama, Kaneoke et al. 2002, Heinrich 2007), but not all studies (Vilhelmsen, van der Weel et al. 2015). Vilhelmsen et al. suggested that their opposing findings might be due to the higher speeds which were above the level used in other studies (Vilhelmsen, van der Weel et al. 2015). They argued that this has its physiological basis in a type of ceiling effect of the number of neurons with a preference for fast speeds which can be saturated; this line of argumentation was indeed demonstrated in macaque monkeys (Maunsell and Essen 1983). Another possible reason is their usage of a virtual road with poles on both sides; maybe the more familiar environment (which also gives cues of the spatial layout via the estimated size of the poles participants are familiar with) and the fact that no fixation cross or dot was present (even though gaze data apparently showed quite good focus towards the centre where the poles appeared) altered the neurophysiological response as especially the amplitude of the visual motion ERP seems to be subject to more modulating factors compared to the latency (Maruyama, Kaneoke et al. 2002). Another important difference between Experiment 2 and Experiment 3 is the lateralization of the N2 component which was only present in sitting participants (see discussion of Experiment 3). It needs to be discussed, why we only found a modulation of the amplitude in Experiment 3 and not in Experiment 2. The most obvious explanation would be the differences in postural demands between the two experiments (see above). Another contributing factor might be the data quality: in Experiment 2, while the trial number was slightly higher, there was no chin rest condition and the number of participants was considerably lower, and it is therefore quite possible that the EEG data was just too noisy to show this specific finding. It furthermore needs to be kept in mind that motion-related VEPs are subject to high inter-individual variability of the overall shape and latency (Kubová, Kuba et al. 1990). This did not affect the agency effect, because this was much more pronounced and highly robust but might mask less marked findings. Most positive neurophysiological results point towards the relevance of the parietal lobe; it must however be emphasized that the parietal lobe is a diverse, heterogenous brain region. In fact, the ‘parietal lobe’, which is mainly a macroscopic

anatomical label, consists of many different areas with distinguishable cell populations, anatomical connections and functions spanning a wide spectrum of functions related but not limited to spatial perception such as experience of presence, navigation, spatial processing, ego- and allocentric representation of space, and visuo-motor control (Maguire, Burgess et al. 1998, Kober, Kurzmann et al. 2012), to name just a few.

7.5 Postural level

The usage of a head-mounted accelerometer comes with some disadvantages compared to other postural measurements. Firstly, it is not possible to dissociate different sub-components of postural stabilization such as head-on-trunk from hip - and ankle sway (Winter, Prince et al. 1996). Another downside is the limited consensus in the literature on appropriate filter settings and data processing in general of this type of postural data. Our filter selection was based on visual inspection and we kept them the same for both experiments to increase consistency and avoid over-interpretation of findings which might be related to the settings. As previously described by Fujimoto and Ashida, sitting and standing participants in our experiments showed different visual induced postural responses to optic flow (Fujimoto and Ashida 2020). There was neither an effect of vection, nor speed nor agency on visual induced postural responses in Experiment 2 and 3 while we observed a stabilization of the forward postural response elicited by the button press in sitting participants in Experiment 3. In both Experiments 2 and 3, participants swayed first forward at around optic flow onset (more prominent in Experiment 3) and directly afterwards backward (more prominent in Experiment 2). The differences in the relationship between forward and backward sway are probably attributable to the different postures. Closer observation of the postural responses in Experiment 2 showed an unexpected difference in sway in fast versus slow as well as high versus low vection trials following optic flow offset which are thought to be related to the head - and body movement during speed estimations. This is discussed in more depth in the discussion section of Experiment 2. Even though many studies have shown modulated postural responses during vection (Kuno, Kawakita et al. 1999, Fushiki, Kobayashi et al. 2005, Palmisano, Apthorp et al. 2014), we did not find any alterations in postural responses caused by or related to differences in vection intensity. This might be due to the short trial duration: the visual information drawn from the optic flow might be used directly to change posture in a form of a visuo-postural reflex arc in the form of e.g. visual stimulation leading to changes in muscle

activity in the legs after less than 100 ms (Lestienne, Soechting et al. 1977, Nashner and Berthoz 1978, Berthoz, Lacour et al. 1979, Fujimoto and Ashida 2020); the rapid changes in visual information might have led to more reflexive postural response which obscured postural changes due to vection onset. A study using more stable visual stimulation and analysing sway at or around perceptual switches from perceived object to self-motion might yield clearer results. Contrary to the reports by Guerraz et al., we did not find reduced postural responses to the more expected stimuli (Guerraz, Thilo et al. 2001). There were however some important differences between their study and ours. Firstly, they used lateral optic flow caused by mechanical displacement of a screen with fluorescing disks compared to the radially-expanding digital optic flow with another order of magnitude of moving dots. This might be important based on observations by Warren et al. that participants change their navigation strategy based on the amount of available optic flow (Warren, Kay et al. 2001). Secondly, they did not measure head- and body acceleration but rather displacement. A third difference is that the speed of optic flow was always the same in their study while it was unpredictable in both the passive as well as in the self-initiated condition. However, they also observed a reduction of the postural responses in a self-initiated condition in which the timing of onset and the speed of the optic flow were known but the direction was randomly selected (albeit with a weaker reduction). For Guerraz and colleagues, the relevant factor underlying the postural stabilization is neither self-specific nor related to the full predictability of the subsequent stimulus (e.g. directionality does not seem to be too important). They assume rather that the predictability of onset timing is what matters most, further supporting the fundamental idea of our study to dissociate the expectations of stimulus onset timing (which was predictable in our self-initiated conditions) and the expectations about stimulus characteristics (e.g. speed was unpredictable in both the self-initiated and the passive condition). Therefore, one must assume that we did not find a reduced postural response either because the unpredictability of the direction is less important than the unpredictability of speed, because postural responses in the anterior-posterior direction and in the medial-lateral direction are controlled differently (Winter, Prince et al. 1996), or because of the participant number which was considerably lower in their experiments compared to ours. However, those questions should be addressed in future studies.

7.6 Combined EEG and postural measurements

In general, one trend in navigation research is to move out of the lab and into ever more complex real-life scenarios (Park, Dudchenko et al. 2018), ideally while recording mobile EEG (Ehinger, Fischer et al. 2014, Dowsett, Dieterich et al. 2020). A big advantage of a head-mounted wireless accelerometer as we used it, is that it allows relatively free locomotion in the range of data transmission (which could in principle be extended by the usage of e.g. a mobile computer). Additionally, the setup as such is also much more mobile than Centre Of Pressure measurements or 3-D magnetic search coil systems e.g. (Guerraz, Thilo et al. 2001).

Experiments 2 and 3 demonstrated that EEG is in principle able to detect the most relevant effects under challenging conditions (i.e. standing, no chin rest, postural responses of head and body). However, until now, it is unclear whether the results which vary between Experiment 2 and 3 (N2 amplitude modulation with different speeds in Experiment 3 and ERD modulation with different speeds / vection intensities in Experiment 2), were only present in one study because of differences in statistical power (i.e. higher noise and lower participant number in Experiment 2) or because of fundamentally different processing of visual motion information caused by e.g. different postural demands. This highly relevant question should be answered in future studies to increase our overall understanding of the influence of different postures on perception, postural responses, and neuronal processing; and indeed, a growing body of research is dedicated to answering this (Guterman, Allison et al. 2012, Park, Dudchenko et al. 2018, Fujimoto and Ashida 2020).

7.7 Summary

We performed several experiments to find out whether self-initiation modulates the behavioural, neurophysiological and postural responses to optic flow in healthy participants. As previously described, the exposure to optic flow led to a prominent ERD over the bilateral parieto-occipital cortex. We were able to demonstrate that, as hypothesized, this ERD is attenuated when the optic flow is self-initiated. In line with this finding, we were also able to identify a negative deflection in the ERP recorded during self-initiated trials between 130 and 170 ms after optic flow onset. Both could be shown in sitting as well as in standing participants. The button-presses to start the optic flow by themselves led to postural sway which was stabilized in the self-initiated condition in

sitting participants. In the standing subjects this sway component had a slightly different shape with an accentuated backward component. Generally, the induced postural responses show distinct patterns in sitting and standing subjects.

8. Clinical aspects

As already mentioned in the introduction, it seems as if the human motor control system, the dynamic coupling between action and perception, and multimodal sensorimotor predictions are deeply interconnected. The symptoms of a wide range of neurological and psychiatric disorders can be better understood in the light of the different aspects of this work.

8.1 Motion sickness

The importance of understanding the relationship between vection and motion sickness as well as the foundation for those two overlapping but probably nonetheless dissociable phenomena has already been discussed in the paper as well as the introduction of this thesis. Here, the focus will be on the role of vestibular disorders on motion sickness susceptibility and relevant pre-requisites. Ebenholtz proposed that the only absolute pre-requisite for the experience of motion sickness is a functioning vestibular system (Ebenholtz 1992); this statement was based e.g. on findings by Cheung et al. who demonstrated that bilateral labyrinthine defective (BVL) subjects were able to experience vection but no VIMS (Cheung, Howard et al. 1991). Walter et al. have shown a general reduction in motion sickness susceptibility for patients with uni - or bilateral vestibular lesions compared to healthy controls while the patients' vection onset latency was shorter (Walter, Fred et al. 1999), both in line with the sensory conflict theories as discussed earlier. Kennedy et al. reported that BVL passengers did not experience motion sickness even in very nauseogenic situations such as sea travel under very severe weather conditions which were able to induce symptoms in all healthy passengers (Kennedy, Graybiel et al. 1968). Also, the exposure to zero gravity elicited markedly less symptoms in BVL patients (Kellogg, Kennedy et al. 1964); however it must be remarked that some of the patients in the respective study might have had at least some residual function and the reduced but albeit present symptoms can be attributed to the remaining vestibular signals. Blind people, in contrast, do experience motion - and sea sickness as non-sensory deficient subjects would (Graybiel 1970). Following the argumentation by Ebenholtz, it is most probable that motion sickness in general and especially visually-induced motion sickness, are elicited by a combination of the presence of a functioning vestibular system (with adequate vestibular stimulation) as a pre-requisite and appropriate visual stimuli as a trigger (Ebenholtz

1992). While vision might not be the most important cause of motion sickness, it becomes increasingly important given the recent rise of e.g. VR technologies, the widening usage of public transportation and the development of self-driving cars (see also Chapters 1 and 3). In this context, not only the nausea related symptoms are of importance which tend to be in the foreground of discussions because of their open visibility, but also less apparent symptoms like the sopite syndrome with symptoms such as excessive drowsiness, lassitude, lethargy, mild depression, and reduced ability to focus on an assigned task following the prolonged exposure to motion (Graybiel and Knepton 1976, Matsangas and McCauley 2014), loss of dynamic visual acuity and postural disequilibrium can pose risks for health and wellbeing (Lawson 2014) on the one hand and efficiency on the other hand.

The most effective treatment options for the nausea - related symptoms of motion sickness on the short-term are scopolamine and antihistamines. On the long-term, adaptation via controlled exposure to the relevant stimuli presents the most promising approach (Golding and Gresty 2015). The classical adaptation phases during exposure to unusual moving environments were described by Reason (Reason 1978) and start with the ‘initial exposure phase’ in which participants are exposed to a combination of vection, multimodal stimulation and resulting sensory mismatch; the (visual-induced) motion sickness onset latency in this phase largely depends on both individual susceptibility factors and stimulus characteristics. In the ‘phase of continued exposure’, the predictions and expectations are updated, re-arrangement in the nervous system takes place, illusory percepts like vection diminish, and adaptation occurs. The following ‘after-effect phase’ takes place after return to the typical environment (e.g. going ashore after some time on the sea or at the destination of a coach journey). This phase is typically accompanied by (physiological) reactions similar to those during the ‘initial exposure phase’ but in the opposite direction of the perceived motion (classical example is the suddenly stopping rotating chair with vestibular stimulation in the opposite direction due to inertia in the vestibular organs). Those reactions typically subside rapidly in most individuals, but some develop mal-de-débarquement syndrome, the persistent, disturbing subjective perception of self-motion after prolonged exposure to passive motion (Van Ombergen, Van Rompaey et al. 2016). As demonstrated by Reason and Brand, long term retention of adaptation seems to be feasible and is more effective the more often the patient was exposed to the environment (Reason and Brand 1975, Reason 1978). Reason and Brand furthermore suggested that adaptation was more

generalized the longer each session lasted (Reason and Brand 1975) and Reason showed that adaptation especially to the exposure to visual triggers was more effective if the (visual) stimulation followed active compared to passive movements (Reason 1978); interestingly, especially in the context of this thesis, they report findings that the remote-control (e.g. by button-press) condition was even more effective than the active movement condition.

8.2 Persistent postural – perceptual dizziness

A typical dizziness disorder often presenting to vertigo and dizziness clinics, 'persistent postural-perceptual dizziness' (PPPD), is thought to result from an insufficient adaptation (Powell, Derry-Sumner et al. 2020) caused by problems with internal predictions due to a persisting or newly emerging mismatch between efference copies and sensory feedback following disruptions or lesions after a vestibular insult (Brandt 1996). PPPD is generally considered a chronic functional condition which includes symptoms such as dizziness or non-spinning vertigo following self-motion; symptoms are often elicited in environments that contain complex or moving visual stimulation and are commonly exacerbated in upright posture (Dieterich and Staab 2017, Staab, Eckhardt-Henn et al. 2017, Popkirov, Staab et al. 2018). Powell et al. suggested, based on findings from their questionnaires, that PPPD may exist on a spectrum extending into the healthy population with a high prevalence (Powell, Derry-Sumner et al. 2020); their results propose subclinical alterations in the multisensory integration related to posture and self-motion perception which predispose healthy individuals and patients presenting with acute vestibular disorders for the development of PPPD. Our experimental design from Experiments 2 and 3 might be further developed to see whether it might be usable as a sensitive tool in screening for those vulnerable individuals looking e.g. at excessive visually-induced postural responses or stronger ERDs induced by the exposure to optic flow and whether the dissociation in active and passive trials might be able to demask vulnerability. This would be plausible given our findings that self-initiation leads to modulated processing in the form of sensory attenuation.

Early intervention using e.g. specialised physical therapy (Popkirov, Staab et al. 2018) after vestibular insults in patients identified as vulnerable might prevent the development of clinical PPPD (Powell, Derry-Sumner et al. 2020). The basic idea behind this approach in vestibular rehabilitation as a special example is that patients with disturbances or lesions in their vestibular or proprioceptive system, like the very common

polyneuropathy in the elderly (Hanewinckel, van Oijen et al. 2016), often rely a lot on their visual system to (learn to) compensate and perform activities of daily life (Paulus, Straube et al. 1984); vection has been proposed to facilitate VR-supported neurorehabilitation while VIMS has been identified to be a potential hurdle on the way to the full potential of the method (Riecke 2006, Palmisano and Riecke 2018, Keshavarz, Murovec et al. 2021). While visual information is often used to compensate for problems in the other systems involved in postural control, reduced visual acuity also leads to increased postural instability; this instability can be measured using posturography but does mostly not lead to clinical symptoms during the normal activities of daily life (Paulus, Straube et al. 1984).

8.3 Optic ataxia

Optic ataxia, first described by Rezso Bálint (Bálint 1909), is a prototypical example of a disorder caused by disturbed motor control in the absence of primary sensory or motor deficits and normal motor awareness (Frith, Blakemore et al. 2000, Andersen, Andersen et al. 2014). Patients have problems in visually guided grasping of objects, due to difficulties with the coordination of visual information and the required finger- and arm movements (Andersen, Andersen et al. 2014), especially with covering the correct distance, correct orienting of the hand and opening the fingers correctly for the object (Jeannerod, Decety et al. 1994, Frith, Blakemore et al. 2000). Patients are aware that it is their own hand which is moving, following their intentions and patients are able to move their hand more smoothly and more precisely given cues from other sensory modalities such as proprioception (Andersen, Andersen et al. 2014) or memory, i.e. very familiar objects (Jeannerod, Decety et al. 1994). Frith et al. suggested that the underlying cause is a disturbed ability to make online corrections to the movements based on visual feedback (Frith, Blakemore et al. 2000), in line with the ‘online control’ theory of optic ataxia (Andersen, Andersen et al. 2014). Patients experience agency over their arm movements but there is still a mismatch between intention, movement plan, and motor prediction on the one side and the actual performed action as perceived by the sensory consequences on the other side. Sensory modulation as studied in our experiments might be a contributing mechanism which could be disrupted in patients with optic ataxia. The reduced modulation of visual feedback to self-initiated movements might impair online control, thereby reducing precision and accuracy. This idea could be tested by comparing the VEPs of patients with optic ataxia and healthy

controls with a setup similar to the one used in our study. If sensory modulation would be impaired in patients, then the N2 amplitude and the ERD in the active condition should be lower compared to the passive condition.

8.4 Alien hand syndrome

Another quite famous disorder with interesting features is the so called 'alien hand syndrome' (AHS), with a partly opposite phenomenology: the affected limbs move without the patient experiencing the intention to move but with an intact sense of ownership over the hand ("it is my hand but I cannot control it") (Frith, Blakemore et al. 2000). A main difference between the two conditions is that optic ataxia is thought to be caused by difficulties with online updating of the movement plans based on visual information, while in AHS the problems are twofold: 1) the visual feedback, though per se correct, is creating a mismatch with the absent intention in the form of missing efference copies; 2) although the movement plans are thought to be intact, there seems to be a problem with the inhibition of unwanted or unintended actions which are decoupled from the normal dependence on external and internal input (Goldberg, Mayer et al. 1981). AHS can therefore be explained by spontaneous performance of movements of the affected limb, which would normally be inhibited, do not follow the normal pathway for the active generation of movements and for that reason don't elicit the normal subjective experience of being in control of the respective movements.

Its phenomenology makes this disorder an interesting model for the interpretation of Experiment 1 and limitations of the agency judgements; especially the two participants who rated their agency to be almost zero in the instructed condition. If we had asked those participants whether their experience resembled the AHS, they would supposably say that it still felt like they were pressing the button intentionally with their own hand. The important point here is, while most participants rated their experience of control focused on the coupling of motor act and onset of optic flow, we would speculate that the two "outliers" rather rated their experience of control over the direction of optic flow. This reflects an important linguistic pitfall in theories of free will: while "I had no choice / alternative to do A and cause B" is a very common way of defending oneself or of refusing to accept responsibility for one's actions, very few would deny that it was actually them doing A and causing B. Both, the phenomenology of the AHS and the experience of our participants in Experiment 1, support the theory by Synofzik, Vosgerau and Newen that sense of agency and ascription of (moral) responsibility are

related with intention-action-coupling and perceiving a sense of agency being pre-requisite to perceiving moral responsibility (Synofzik, Vosgerau et al. 2008). In superficial debates on free will, this dissociation is often omitted, leading to the (mis-)conclusion that determinism and moral responsibility contradict each other.

While intuitively most people are able to experience sense of agency in a situation in which they would refuse responsibility over the outcome, this experience is altered in delusions of control. Some patients might lose their sense of agency ("I was controlled by external forces") while others still perceive the intention-action coupling normally but attribute the responsibility to external forces ("I did it because the devil ordered me to do it"). Patients might even assume responsibility for independent events in the external world ("This plane crashed because I forgot to pray").

8.5 Schizophrenia

The most prominent examples of a medical condition presenting with alterations in the sense of agency as well as in various other domains, are disorders from the schizophrenia spectrum. Studies have shown differences between patients and their close relatives compared to healthy controls on many levels of cortical visual processing (Pamela D. Butler, Isaac Schechter et al. 2001), and specifically relevant for our work, in motion processing (O'Donnell, Swearer et al. 1996, Stuve, Friedman et al. 1997, Chen, Nakayama et al. 1999, Chen, Palafox et al. 1999); a good overview can be found in the review by Chen (Chen 2011). Those subtle alterations can eventually be observed even before the onset of clinical schizophrenia (Antígona Martínez, Pablo A. Gaspar et al. 2018). In line with disorders discussed earlier, Hong et al., using a speed discrimination task, suggested that it is not the motion perception per se which is altered, but rather the generation or integration of feedback following eye movements (Hong, Turano et al. 2009). Additionally, patients diagnosed with schizophrenia seem to show a higher motion sickness susceptibility (Mirabile and Glueck 1980, Brandt 1996).

In the treatment of schizophrenia, it is generally assumed that the later the diagnosis of the disorder is made and therefore the longer the delay to the beginning of treatment, the higher the risk for a chronic course and the higher the risk for treatment resistance (Klosterkötter, Ruhrmann et al. 2005, Cannon, Cornblatt et al. 2007, McGorry, Killackey et al. 2008, Schultze-Lutter, Ruhrmann et al. 2009). Core features of schizophrenia are disturbances of the self with first rank symptoms related to impaired sense

of agency as well as altered self - / other barriers as shown in both phenomenological and behavioural studies (Kozáková, Bakštein et al. 2020). Not only alterations in motion perception as mentioned above, but also an impaired sense of self can be observed across the full schizophrenia spectrum as well as in non-psychotic relatives, in whom they are associated with an increased risk of transition into the schizophrenia spectrum (Parnas, Raballo et al. 2011). Self-disorders are profound, trait-like distortions of subjective experience with an unstable sense of presence, a lack of a basic sense of self-identity, and alterations in the implicit knowledge of familiarity and meaning. Those fundamental experiences are generally taken for granted in the patient's cultural environment and are tacit aspects in the experience of being self-aware (Parnas, Bovet et al. 2002, Sass and Parnas 2003, Parnas, Raballo et al. 2011). While those descriptions focus on the phenomenological aspects, from the perspective of the patient, the same phenomena are commonly studied in the context of sense of agency under the terms: 'delusions of control' and 'passivity experience'. Patients with schizophrenia often experience their actions, thoughts or emotions as belonging to or being forced upon them by someone else (Frith, Blakemore et al. 2000). From the viewpoint of agency research, those features can be interpreted as situations in which e.g. the performed and the intended action match without the patient feeling as if they were in control and without the emergence of a normal sense of agency (Frith, Blakemore et al. 2000). Spence suggested that the problem might lie in disturbances of the normal temporal structure of awareness of initiating a movement followed by the sensory consequences of the action (Spence 1996); and indeed, patients with delusions of control seem to experience the initiation different or too late. In a later study, Spence et al. described a hyperactivity in the right inferior parietal cortex of patients diagnosed with schizophrenia who were presenting with delusions of control (Spence, Brooks et al. 1997). Frith et al. proposed that this hyperactivity might be indicative of a problem with the internal prediction mechanisms underlying the emergence of a sense of agency (Frith, Blakemore et al. 2000), as a sensory attenuation in response to predictable self-generated stimuli would be expected in this region.

Parnas et al. suggested the assessment of, and screening for, self-disorders as a potential approach allowing to identify those patients with vulnerability traits to ultimately allow earlier diagnosis and treatment of patients with schizophrenia spectrum disorder (Parnas, Raballo et al. 2011). In the light of the findings by e.g. Spence et al. (Spence,

Brooks et al. 1997) and the growing literature on altered motion processing and especially the demonstration that this can even be observed before clinical onset of schizophrenia (Antígona Martínez, Pablo A. Gaspar et al. 2018), it would be worth testing the prospects of using our combination of either self-initiated or passive optic flow and their neurophysiological consequences and further investigate their potential in assessing e.g. the transition risk to full clinical schizophrenia in at risk individuals or anticipate the prognosis in first-episode psychosis.

8.6 Phantom limbs

Another type of disorder gives insides into the processes underlying motor awareness. Following earlier work (Ramachandran and Rogers-Ramachandran 1996, Frith, Blakemore et al. 2000), it is not uncommon that patients with phantom limbs report being able to voluntarily “move” their phantom, especially as long as the limb was not paralyzed before amputation. This is thought to result from a combination of different processes (Frith, Blakemore et al. 2000): firstly, neural plasticity and reorganization of the de-afferented cortical region can provoke a situation in which somatosensory stimulation of more distant skin areas might be co-interpreted as resulting from stimulation of the phantom. Secondly, especially shortly after the amputation, a stream of motor commands will still be generated, and this might be used to (wrongly) predict the position of the (absent) limb, leading to the sensation that it is still present and might even be movable (Ramachandran and Rogers-Ramachandran 1996). Further evidence for this explanation comes from another phenomenon: the sensation of additional or supernumerary limbs (Hari, Hänninen et al. 1998): this experience is probably based on a malfunctioning integration of the motor commands and the sensory information including the feedback which leads to the situation in which the motor commands are used to predict the position of e.g. the right arm following a movement and the sensory information which might be delayed, interpreted as if the same arm was static. The mismatch is then interpreted as if two versions of the arm existed (Frith, Blakemore et al. 2000). In line with this theory, suggesting the role of motor commands for position estimation, the third arm only followed active or voluntary, but not passive movements of the arm (Hari, Hänninen et al. 1998, Frith, Blakemore et al. 2000)). Frith et al. postulated that the opposite happens in anosognosia in the domain of motor control, a condition in which the patient is not aware that their limb is paralyzed (Frith, Blakemore et al. 2000); according to Heilman et al., patients with this form of anosognosia do not

generate efference copies, and therefore don't experience the mismatch between ineffective motor commands and the missing sensory feedback (Heilman, Barrett et al. 1998). Frith et al. proposed as an alternative explanation that efference copies are normally generated but the mechanism underlying the comparison between motor command and sensory feedback is faulty (Frith, Blakemore et al. 2000). This second approach also explains the observation that some patients experience their movements like i.e. clapping as successful even if they only make clapping movements with the healthy hand (Ramachandran 1996); those patients might experience and form the intention normally including efference copies and perform it with the healthy hand while no mismatch and therefore no error signal arises from the action of the paralyzed hand. Except for the missing visual and auditory feedback which might be left unnoticed given the common comorbidity with hemineglect (Frith, Blakemore et al. 2000) or the general tendency to be less aware of our motor performance than we would assume which can also be observed healthy subjects (Fourneret and Jeannerod 1998), the combination of those aspects might lead to the absence of a signal indicating the ineffectiveness of the movement which is consequently interpreted as being performed successfully.

The control over the phantom limb via motor commands tends to vanish over time due to adaptation and learning processes (Frith, Blakemore et al. 2000). Repetitive usage of mirrors can however be used to regain control over the phantom limb which is an important method in the treatment of phantom pain; phantom pain is often caused or at least accompanied by the sensation of the limb being fixed in a painful, unnatural position (Ramachandran and Rogers-Ramachandran 1996). Based on those findings it can be assumed that it is also possible to link motor commands to actions and movements in virtual environments (Haggard 2017) which perhaps increases immersion and effectiveness of VR or one step further: those virtual environments might even offer opportunities for neurorehabilitation e.g. training of motor functions following i.e. spinal cord injury or navigation skills after a stroke.

9. Future Work

This section will focus on future basic scientific work while potential clinical applications and translational work were already discussed in Chapter 8.

9.1 Lateralization

Our third experiment showed a lateralization of the putative effect of self-initiation on the ERD which was not present in the second experiment, in which the difference between the ERD in active and passive could be observed over both hemispheres. Furthermore, we also found a lateralization of the motion-onset VEP of the pooled conditions with the N2 amplitude being significantly higher over the left hemisphere. Future studies should test whether this is because of e.g. differences in the postural demands, in the multisensory input and integration during standing and sitting (Fujimoto and Ashida 2020) or due to the differing EEG quality which was arguably better in Experiment 3. The EEG quality could be increased by focusing more on the parietal areas of interest, using more local channels to further increase the spatial resolution and extend the analysis to source localizing procedures (Cohen 2014). Apart from improving the quality and specificity of the input data, this can be done by comparing the ERDs across both hemispheres in different postural settings with a mobile EEG setup, e.g. sitting on a more stable chair with the legs on the floor, our bar chair, standing on firm or foam ground which could further increase the postural demand. Other options would be to look at more complex simulators, driving or real life locomotion such as walking (Ehinger, Fischer et al. 2014, Dowsett, Herrmann et al. 2020). The effects of different postural and navigational tasks on the neurophysiological responses and the visuo-vestibular interaction to the same experimental task and visual stimulation could further elucidate the generalisability of our findings; to examine this makes sense as e.g. Fujimoto and Ashida demonstrated that the same visual stimuli, shown in different postures, can lead to different postural and probably also neurophysiological responses (Fujimoto and Ashida 2020). One step further would be to not only introduce variance in the postural demands but also vary the visual stimulation and move away from the highly abstract stimuli we used which however inarguably have their advantages, and go over to more naturalistic VR settings (Riecke 2006, Vilhelmsen, van der Weel et al. 2015, Riccelli, Indovina et al. 2017) or even leave the lab (Park, Dudchenko et al.

2018). Another important future step will be the usage of coherent and incoherent multisensory input (Ehinger, Fischer et al. 2014) which is either self-initiated or passively presented. Such a design could offer insights into the dynamical weighting and integration process of the different sensory modalities (Wright, DiZio et al. 2005).

9.2 Self-initiation in locomotion

Those different postural tasks can be combined with the research question on what actually counts as self-initiation in locomotion and self-motion processing. Our button-press / finger movement, for example, is per se not a motor response that is involved in postural control whereas a head turn or leaning forwards would be. The fact that those actions are directly part of vestibular reflex loops could modify the resulting responses. This would be an important basis to gain a better understanding of the situations in which one could expect to find sensory attenuation in the visual motion processing domain and the even more fundamental question: whether the underlying mechanism behind sensory modulation of the sensory feedback to self-generated stimuli can be attributed to self-specific or general predictive mechanisms (Kaiser and Schütz-Bosbach 2018). This question bares probably even more relevance for the traditional agency research and should be answered by classical, securely established experimental paradigms.

9.3 Vection sensitization

Another interesting line of research would be to further illuminate the so called ‘vection advantage’ with the aim to ameliorate the user experience and spatial cognition in virtual environments (Riecke 2011, Riecke, Feuereissen et al. 2012, Palmisano, Allison et al. 2015) and explore the possibilities this might offer for training and neurorehabilitation. Examples would be e.g. the training of spatial memory (Montana, Tuena et al. 2019) or motor-cognitive training after a stroke (Perez-Marcos, Bieler-Aeschlimann et al. 2018)); our studies are especially interesting in this context as they are consistent with the existence of a sensitization effect for vection (Palmisano and Riecke 2018) which is hypothesized to reduce onset latency due to the high number of all expanding optic flow trials without incoherent or reversed direction trials in between; this sensitization effect could be used to make more use of the vection advantage in virtual settings. In line with this idea, further studies should address the exact relationship of

vection and VIMS and their development over time during the exposure to VR. This could be done by using stimuli with properties which allow to dissociate them (Keshavarz, Riecke et al. 2015, Keshavarz, Philipp-Muller et al. 2019) and e.g. ask for vection and VIMS judgments explicitly after each trial. Additionally, it would be interesting to identify more reliable objective markers and analyse whether the level of control 1) influences the two phenomena and 2) if they are modulated differently. The results of those investigations can all be applied to maximize the ‘vection advantage’ while keeping the VIMS inducing properties as low as possible.

10. List of figures

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Appendix

A. Inclusion criteria checklist

LMU LUDWIG-MAXIMILIANS-UNIVERSITÄT MÜNCHEN

Checklist for TS study

Name: _____ Date:_____

	Yes	No
Have you ever had a seizure or do you or someone in your family suffer(s) from epilepsy?	☐	☐
Have you ever been treated for a neurological or psychological illness? e.g., depression, neurosurgery of brain or spinal column, high intracranial pressure, multiple sclerosis, etc.	☐	☐
Have you ever had recurrent fainting spells or circulatory collapse?	☐	☐
____ If yes how often?		
Have you ever had a serious brain trauma followed by loss of consciousness?	☐	☐
Have you ever had a cardiac infarct?	☐	☐
Do you suffer from hearing loss or tinnitus?	☐	☐
——Is there a possibility you might be pregnant?	☐	☐
Do you have any metal fitted in your body? e.g., dental braces, metal plates or screws, hearing aids, cochlea-implants, medication pump, insulin pump, other implanted pump systems, surgical clips, pacemaker, metal fragments, nerv stimulators	☐	☐
Are you taking any medication? (apart from oral contraceptive)	☐	☐
How many hours did you sleep last night?	_____	
How much alcohol have you drunk in the last 24 hours?	_____	
____	☐	☐
Have you already taken part in a TMS study?		
If so, how often and when was the most recent?		
Have you ever experienced nausea, vomiting or headache occuring from blinking lights?	☐	☐

B. Handedness Questionnaire

Which hand you prefer for that activity?
Do you ever use the other hand for the activity?

Which hand do you prefer to use when:		no pref		Do you ever use the other hand?
Writing:	Left ○	○	○ Right	☐ Yes
Drawing:	Left ○	○	○ Right	☐ Yes
Throwing:	Left ○	○	○ Right	☐ Yes
Using Scissors:	Left ○	○	○ Right	☐ Yes
Using a Toothbrush:	Left ○	○	○ Right	☐ Yes
Using a Knife (without a fork):	Left ○	○	○ Right	☐ Yes
Using a Spoon:	Left ○	○	○ Right	☐ Yes
Using a broom (upper hand):	Left ○	○	○ Right	☐ Yes
Striking a Match:	Left ○	○	○ Right	☐ Yes
Opening a Box (holding the lid):	Left ○	○	○ Right	☐ Yes
items below are not on the standard inventory:				
Holding a Computer Mouse:	Left ○	○	○ Right	☐ Yes
Using a Key to Unlock a Door:	Left ○	○	○ Right	☐ Yes
Holding a Hammer:	Left ○	○	○ Right	☐ Yes
Holding a Brush or Comb:	Left ○	○	○ Right	☐ Yes
Holding a Cup while Drinking	Left ○	○	○ Right	☐ Yes

from http://www.brainmapping.org/shared/Edinburgh.php (last access 12.12.2022)

C. Instruction sheet – Experiment 2

Dear participant, thank you for taking part in our experiment!

The instructions are in the text below. If you have any unanswered questions, please feel free to aks the experimenter.

Aim of the experiment
The aim is to find out how good people are at object motion speed judgements and what neurophysiological processes are involved in this task.

EEG - Cap
The cap you are wearing is measuring your head movement and your brain activity.

Procedure and responses
You will be presented 240 trials overall, separated in 12 blocks of 20 trials. In each trial you will be first shown a still display (a picture of this is shown at the end of this page, fig. 1). The dots will start to accelerate (more information in the next section) and then move with a random end speed. After the motion is over (~2s), you will be shown a vertical line and your mouse cursor. Your job is to rate the end speed on the scale from 0 to 100. You just have to move the cursor to the point on the line where you think it fits your judgement and just one click on a mouse button is enough to register your response (it doesn't matter if you click next to the line, only the height will be registered). To make this easier for you, you will be presented three reference speeds, namely 0, 50 and 100, at the beginning of each block.
After answering this question, another line with a new question will appear: Here you are asked to rate your "vection" experience (for a definition look at the bottom of this page). The procedure is just the same as in the question where you had to judge the speed.

Active and passive blocks
The experiment is separated into "active" and "passive" blocks to make it more comparable to other studies found in the literature. In the passive trials, the dot motion will start after a random time without your control. In the active blocks, you are completely in control and can freely choose the time that this starts . In the active blocks the static display (fig. 1) will be shown and the dots will wait for your mouse-click.

Vection here is the experience that you are moving when you are not really. You may have experienced it before, for example during the "train illusion". This may happen sometimes if you are sitting in a still train at a station, and the train next to you starts to move, sometimes causing the illusory feeling that you are moving. People feel vection to different extents. Please rate how much you feel vection during our experiment, with 100 corresponding to "I felt like I was really moving".

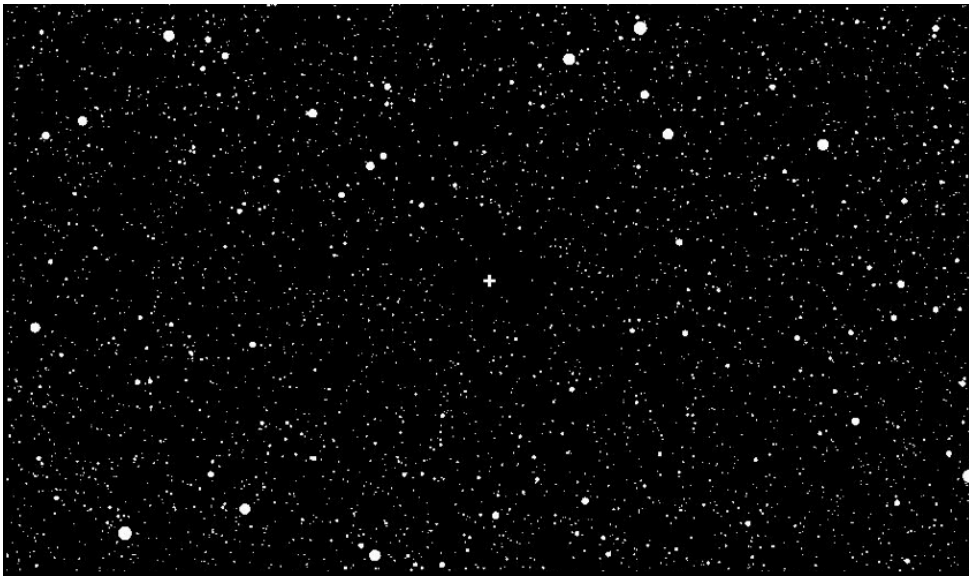

fig. 1

D. Instruction sheet – Experiment 3

Dear participant, thank you for taking part in our experiment!

The instructions are below. If you have any questions, please feel free to ask the experimenter.

Aim of the experiment
The aim is to find out what's going on in the human brain when we are moving through our environment at different speeds.

EEG - Cap
The cap you are wearing is measuring your head - / body movements and your brain activity in areas responsible for visual processing.

Glasses
The custom-built glasses make it easier for you to focus on the screen.

Procedure and responses
You will be presented with **320 trials overall**, separated in **16 blocks** of **20 trials**. In each trial you will be first shown a still display with a **fixation cross** (a picture of this is shown on the second page of this sheet, fig. 2). Please fixate this cross whenever you see it! That means, **keep your eyes on it and don't look elsewhere!** In the beginning the cross will be white. One second later it turns red. After a little time the cross will change its color to white again and shortly thereafter, the dots will start to accelerate (more information in the next section) and then move with a random end speed. Approximately 2 s later, the motion will stop and you will see the **static display** (fig. 1) again for ~ 1 s. Next, you will be shown a vertical line and your mouse cursor. Your job is to rate your personal **vection**[1] experience during this trial on a scale from 0 to 100. You just have to move the cursor to the point on the line where it best fits with your experience. Just one mouse-click and done: your judgment is registered (it doesn't matter if you click next to the line, only the height will be registered). At the beginning and end of the experiment during the **Resting-State Recording**, you have to either **look on a static display** (fig. 2) and fixate on the white cross or you will be asked to **press the left mouse button** whenever the fixation cross turns first red and then white again while also fixating the cross. Afterwards there will be five active and five passive trials in the **practice block** to help you get familiar with the task. The subsequent experimental blocks will be divided in **active / passive** and **chin-rest / no-chin-rest** blocks in randomized order and different combinations of the conditions. In between blocks you will be asked to **verbally report your motion sickness level**[2]. After that, please **take breaks**, drink a little water and relax. Please feel free to take your time! If you feel well and not too tired, our data is better as well, so it is a win-win situation!
We will finish the experiment with another 6 min of **Resting-State Recording**.

Active and passive blocks
The experiment is separated into "active" and "passive" blocks to make it more comparable to other studies found in relevant literature. In **passive** blocks, the dot motion will start after a **random time interval** following the **color change** of the fixation cross without your control. In active blocks, you are completely in control and can freely

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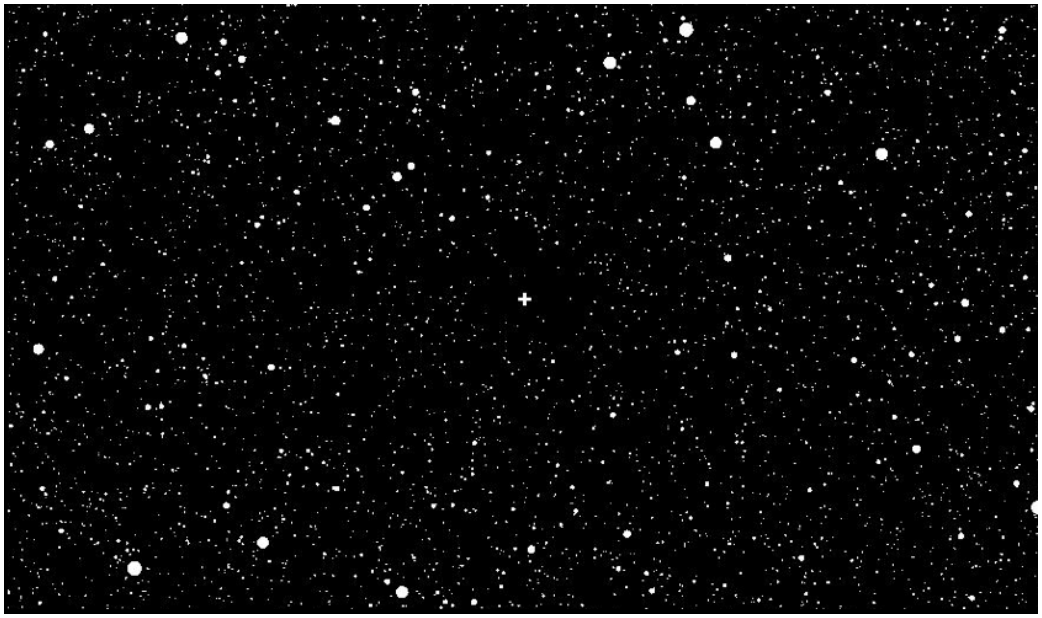
[1] **vection** here is the experience that you are moving when you are not really. You may have experienced it before, for example during the **"train illusion"**. This may happen sometimes if you are sitting in a still train at a station, and the train next to you starts to move, sometimes causing the illusory feeling that you are moving. People feel vection to different extents. Please rate how much you feel vection during our experiment, with **100 corresponding to "I felt like I was really moving"**.

[2] **motion sickness** is characterized by **general discomfort**, **nausea**, and **stomach problems**. Maybe you have experienced those and other symptoms once in public transport or on a boat. Please rate your experience on a scale from **0** meaning **'no sickness at all'** to **20** meaning **'frank sickness'** and ignore other sensations like nervousness, boredom, or fatigue in your rating (1).

choose the time to start the dots at **any time you want** after the **second color change**[3]. In the active blocks the static display (fig. 2) will be shown until your mouse-click.



(fig. 1)

(fig. 2)

(1) Behrang Keshavraz and Heiko Hecht, “Validating an Efficient Method to Quantify Motion Sickness” (2011)

[3] In each trial and during the Resting-State recording, the fixation cross will be white in the beginning. After 1 s, the cross will turn red. The red cross will again be replaced by a white one after a random time (0.5 - 1 s).

Acknowledgements

This work was financially supported by the Munich Center for Neurosciences (MCN), the German Federal Ministry of Education and Research (BMBF 801210010-20) and the DFG (TA 857/3-2). During my time as a medical and doctoral student, I received a scholarship from Konrad Adenauer Stiftung which allowed me to focus on my studies and my scientific work. I also profited from the annual KAS natural sciences network meeting, where I could discuss my ideas and present aspects of my work in an interdisciplinary setting.

I would like to thank my supervisor Paul Taylor for everything I could learn from him during our more than 6.5 years of working together. When I first met him, I was struck by his profound knowledge, his curiosity, and his deep love for the scientific exploration of the human mind and brain. He guided me in a way that allowed me to take responsibility for my decisions and make my own mistakes while never letting me feel alone. He motivated me to work hard without ever pushing. I could not have wished for a better guide into academia and the world of science. And, I will never forget his inspirational seminars on “Higher Vestibular Disorders” and “Cognitive Neuroscience of Consciousness”.

I also want to thank James Dowsett, my Co-Supervisor who introduced me to stimulus design and opened the door for me into the world of programming. James was always an inspiring colleague with his creative, smart and pragmatic soft- and hardware solutions without which a lot of our lab’s scientific projects would not have been feasible.

Paul’s working group and my colleagues at the “Forschungshaus” always were a collection of curious, motivated and talented people. I really enjoyed discussing science and working with all of them, especially with Angela Mastropasqua, Lina Willacker, Fernando Cross-Villasano and Michaela McAssey who was the person to infect me with the interest for vection with her powerful roll vection stimuli. A big thank you to Ainhoa Mongelos Garcia, our working student who assisted me with data collection during Experiment 3.

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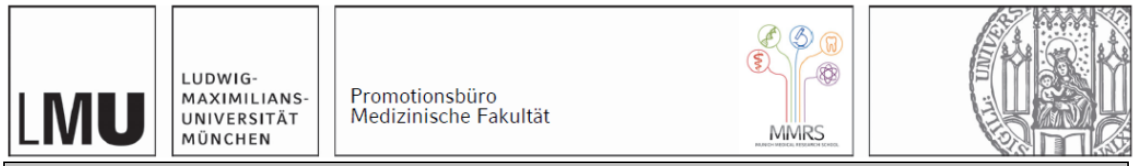
It is a rare gift to have parents who support you in all situations with all they have. Parents who believe in you, who are proud of you no matter what you do. Thank you Beate and Michael Obereisenbuchner, for being always there for me and for accompanying me on my path since the first day.

This work would probably not have been started in the first place without my best friend and partner, Christine Spieker. The idea for the first experiment, back when I was an intern in Paul's working group, was born following a Christmas present I received from her in 2016. I got tickets for a flight simulator with her as my co-pilot. While I was "landing the plane", she told me that she experienced quite intense vection which I did not feel to a comparable degree. After discussing our diverging experiences following the same visual input, I started searching the literature for similar reports or studies already done on this matter. When I found little information on sensory attenuation of the experience of vection but a lot of literature suggesting its theoretical plausibility, I went to discuss this idea with my supervisor Paul. He was enthusiastic and we started planning the first experiment right away. But Christine's contribution does not stop there. Her analytical mind, her intelligent remarks and our conversations about statistics as well as my theoretical reflections, helped me sort out my thoughts in a way which would not have been possible without her. Her emotional support during frustrating and seemingly unfruitful episodes of my research always kept me going. Thank you for everything (including enduring the evenings and weekends I spent in front of a laptop or in the lab).

Finally, I would also like to thank all the participants who chose to take part in our experiments. Especially in the field of cognitive neuroscience it is sometimes unavoidable to ask human subjects actively about their perception. Without curious participants and the concept of "Versuchspersonenstunden", all of this would hardly have been possible.

Affidavit



Eidesstattliche Versicherung

Obereisenbuchner, Florian
Name, Vorname

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation mit dem Titel:

„The Effects of Expectancy and Control on the Perception of Ego-Motion in Space: a combined Postural and Electrophysiological Study“

selbständig verfasst, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

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