EEG ANALYSIS OF VISUALLY-INDUCED VECTION IN LEFT- AND RIGHT-HANDERS

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SUMMARY

Our ability to perceive and control self-motion is fundamental to our capacity to successfully navigate and interact with our environment. Distinguishing between our own motion and the motion in our environment presents a complex problem for the brain, requiring the weighting and integration of information from multiple sensory systems. This thesis investigated the neural mechanisms by which self-motion is discriminated by examining electroencephalography (EEG) activity during large-field visual motion stimulation that induces so-called vection perception. Vection is an apparent sensation of self-motion that relies heavily upon reciprocal interaction of the visual and vestibular systems. A lateralization of cortical multisensory vestibular processing is well established, with left-handers exhibiting a left hemisphere dominance and right-handers exhibiting a right hemisphere dominance. It is unclear whether this handedness-dependent lateralization of multisensory vestibular processing affects vection processing and/or perception. Therefore, this thesis had two aims: 1) to apply EEG techniques to the study of vection perception and 2) to examine the potential hemispheric lateralization of vection processing in left- and right-handers. To this end, two experimental studies were conducted.

The first study investigated the behavioural characteristics and neural oscillations associated with vection perception in left- and right-handers. Participants were exposed to vection-inducing visual motion stimulation and to a novel control stimulus. Online EEG was recorded and vection perception was assessed in real time. The findings showed no differences between left- and right-handers on behavioural measures of vection, indicating that both groups experience vection comparably. Further, both left- and right-handers exhibited a decrease in centro-parietal alpha power during exposure to vection-inducing visual motion stimulation. However, the topography of this effect was handedness-dependent, with left-handers showing a decrease over left lateralized centro-parietal electrodes and right-handers showing a decrease over bilateral midline centro-parietal electrodes. Further analyses, time-locked to vection onset, revealed that both left- and right-handers showed a trend of decreased alpha power around the time of vection onset and increased alpha power during ongoing vection perception. Altogether, this study demonstrated that: 1) left- and right-handers experience comparable vection perception despite exhibiting vection-related processing at different topographical locations and 2) alpha activity changes appear to follow the temporal dynamics of vection perception, reflecting vection onset and the maintenance of vection perception.

The second study investigated the temporal activation of the vection network by vection-compatible visual motion stimulation and the lateralization of these processes in left- versus right-handers. Analyses involved comparison of the event-related potentials (ERPs) and estimated neural source activity evoked by the onset of visual motion stimulation that reliably induces vection perception (i.e., vection-compatible) against that evoked by the onset of control visual motion stimulation that

rarely induces vection perception (i.e., vection-incompatible). Although vection was present and behaviourally measured in this study, all EEG analyses were time-locked to motion onset, which occurred several seconds before vection onset. Thus, the EEG findings reflect the neural processes that occur *before* vection perception. In both left- and right-handers, vection-compatible motion onset evoked central ERPs with attenuated mean amplitudes in an early (160 – 220 ms) and a late (260 – 300 ms) window. Both groups exhibited differences in estimated source activity across visual, sensorimotor, and multisensory vestibular cortex in the early window, while in the late window differences were primarily located in the posterior cingulate, retrosplenial cortex, and precuneus. Group comparisons in the early window revealed a larger ERP condition difference (i.e., vection-compatible stimulation minus vection-incompatible stimulation) in left-handers and estimated source activity differences between the two groups in the CSv area. Despite these differences in EEG activity, left- and right-handers subsequently went on to experience comparable vection perception. Altogether, this study demonstrated that: 1) vection-compatible visual motion stimulation evokes consistently attenuated central ERPs and interacts differently with visual, sensorimotor, and multisensory vestibular networks (i.e., relative to vection-incompatible stimulation) and 2) ERP and area CSv responses to vection-compatible versus vection-incompatible visual motion stimulation are influenced by handedness.

In summary, by employing EEG techniques to study vection perception and examining the potential hemispheric lateralization of vection processing in left- and right-handers, this thesis enhances our knowledge of vection (i.e., self-motion) perception and its underlying neural mechanisms. The remarkable temporal accuracy of EEG was exploited to disclose the temporal activation of the vection network and to identify vection-specific alpha oscillation modulations. Moreover, it was revealed that left- and right-handers show both similarities and differences in vection processing and perception. Altogether, this thesis has important implications for future research as it highlights the benefits of temporal accuracy and the relevance of handedness in the study of vection (i.e., self-motion) perception and its underlying neural mechanisms.

ABBREVIATIONS

CW	Clockwise
CCW	Counter-clockwise
CMA	Cingulate motor area
CSv	Cingulate sulcus visual area
EEG	Electroencephalography
EHI	Edinburgh Handedness Inventory
(e)LORETA	(exact) Low-resolution brain electromagnetic tomography
ERP	Event-related potential
FEF	Frontal eye field
FFT	Fast Fourier Transform
fMRI	Functional magnetic resonance imaging
IPS	Intraparietal sulcus
IPSmot	Intraparietal sulcus motion area
KO	Kinetic occipital region
LIP	Lateral intraparietal region
LOR	Lateral occipital region
MEG	Magnetoencephalography
MIP	Medial intraparietal area
MRI	Magnetic resonance imaging
ms	Milliseconds
MST	Medial superior temporal area
MT	Middle temporal area
MVS	Magnetic vestibular stimulation
pCi	Posterior cingulate area
PcM	Precuneus motion area
PEc	Part of the anterior precuneus
PET	Positron emission tomography
PIC	Parietal insular cortex
PIVC	Parieto-insular vestibular cortex
PPA	Parahippocampal place area
p2v	Putative 2v area (dorsal postcentral sulcus)
SFS	Superior frontal sulcus region
TF	Time-frequency
VIMS	Visually-induced motion sickness
VIP	Ventral intraparietal area
VR	Virtual reality

TABLE OF CONTENTS

SUMMARY
ABBREVIATIONS

1. GENERAL INTRODUCTION

Our ability to perceive and control self-motion is essential for our successful navigation and interaction with the environment. Ordinarily we simply 'know' when we are moving and when the environment around us is moving. We are oblivious to the fact that distinguishing between object-motion and self-motion actually presents a complex problem for the brain. Multisensory information from visual, vestibular, somatosensory, and auditory systems must be weighted and integrated. Often the information provided by these sensory systems is conflicting, with some information indicating object-motion and other information indicating self-motion. The distinction between object- and self-motion must also be achieved quickly so that we can initiate appropriate behavioural responses in an adaptive and timely manner. Although, there is a long history of research, we still do not fully understand all the mechanisms and neural processes through which object- and self-motion are distinguished in the brain. This thesis contributes to our understanding by examining electroencephalography (EEG) activity in response to large-field visual motion stimulation.

1.1 Visually-induced vection: characteristics, causes, and consequences

Vection is a phenomenon in which a stationary individual experiences an apparent sensation of self-motion. Although vection can be generated through various sensory systems[1], this thesis focuses exclusively on visually-induced vection. A classic, real-world example of this type of vection is the so-called 'train illusion'. This occurs when an individual misinterprets the visual motion cues from the movement of an adjacent train and perceives that they are moving despite their own train remaining stationary. This illusion illustrates that visual cues alone are sufficient to generate self-motion perception. Moreover, the train illusion is not prevented by an absence of congruent vestibular, somatosensory, or auditory cues. This suggests that the visual system not only plays a dominant role in generating self-motion perception but that visual information may supersede conflicting information from other sensory modalities, especially in stationary subjects being transported at constant velocity. The following sections address the key characteristics, causes, and consequences of visually-induced vection.

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[1] For example, auditory (Väljamäe, 2009), haptokinetic (Murata et al., 2014), and biomechanical (Riecke et al., 2011) vection have been reported.

a) Characteristics of vection

Actual self-motion involves movement along various planes and cardinal axes. This movement generates optic flow, which is one of the most important contributors to the perception of self-motion (Pitzalis et al., 2013). Conversely, exposing an individual to patterns of optic flow can induce compelling sensations of vection along different planes and axes (Beer et al., 2002; Brandt et al., 1973; Deutschländer et al., 2004; Pitzalis et al., 2013). For example, optic flow around the line of sight induces roll vection whereas expanding/contracting optic flow induces forward/backward vection. Vection is usually experienced as contra-directional to the presented optic flow (Dichgans & Brandt, 1978), but may also occur in the same direction as the optic flow (Becker-Bense et al., 2012). An important characteristic of vection is that it does not occur instantly, but rather develops over several seconds of visual stimulation (Brandt et al., 1973; Dichgans & Brandt, 1978). The elapsed time between visual motion onset and vection onset is known as the vection onset latency. Moreover, vection perception is not necessarily continuous, even if the visual motion stimulation remains constant. Rather, during prolonged motion stimulation perception tends to alternate between periods of vection and periods of object-motion (Brandt et al., 1974; Dichgans & Brandt, 1978; Kleinschmidt et al., 2002; Thilo et al., 2003). Thus, vection appears to be a bistable percept. Arguably, the most challenging characteristic of vection perception is that it is largely variable across individuals (Brandt et al., 1973; Dowsett et al., 2017; Kennedy et al., 1996). For example, the same visual motion stimulus tends to produce highly variable onset latencies, vection durations, and vection intensities across individuals. This can lead to difficulties in interpreting experimental findings and linking behavioural and neural data. Consequently, the ability of an experiment to generate consistent, stable vection perception across participants is an important, non-trivial component of quality vection research.

b) Causing vection with visual stimuli

Perhaps unsurprisingly, the use of visual motion stimuli that mimic the properties of optic flow produced by actual self-motion is a core cause of vection perception. Such properties may include coherent motion, constant/accelerating velocity, looming, and a point of expansion, but to name a few. Further, including natural visual-field features that occur during actual gait (e.g. horizontal and vertical shifts of the visual stimulation pattern) results in enhanced vection perception (Bubka & Bonatoô, 2010). Large-field visual stimulation is also essential for generating compelling vection (Brandt et al., 1973; Dichgans & Brandt, 1978), with small-field stimulation resulting in comparatively weaker vection perception (Beer et al., 2002; Keshavarz et al., 2017; Previc et al., 2000). Early research demonstrated that vection is most effectively generated by peripheral stimulation (Brandt et al., 1973; Dichgans & Brandt, 1978), although it has also been claimed that central and peripheral stimulation may elicit comparable vection if overall stimulus size is controlled for (Howard & Heckmann, 1989; Post, 1988; Tarita-Nistor et al., 2006). It has also been argued that vection is not driven by central or peripheral stimulation per se, but rather by a foreground-background distinction whereby vection is determined by the part of the stimulus that is perceived as the background (Berti et al., 2019; Howard & Heckmann, 1989; Seno et al., 2009). The use of fixation rather than free gaze has also been linked to enhanced vection perception (Fushiki et al., 2000; Howard & Howard, 1994; Tarita-Nistor et al., 2006).

Top-down cognitive factors such as expectations about self-motion likelihood, the plausibility of actual motion, and semantic meaning attached to the visual stimuli also influence vection perception (D'Amour et al., 2021; Ogawa & Seno, 2014; Palmisano & Chan, 2004; Wright et al., 2006). Although attention has also been linked to vection perception, the exact nature of this association is unclear with some evidence indicating enhanced vection when attention is withdrawn (Kitazaki & Sato, 2003; Trutoiu et al., 2008) and other evidence suggesting that the withdrawal of attention impairs vection (Seno, Ito, et al., 2011). Individual participant factors such as personality traits and characteristics may also influence vection perception (D'Amour et al., 2021; Seno, Yamada, et al., 2011). Lastly, vection perception varies across the lifespan, with stronger vection typically occurring in children and younger adults (Haibach et al., 2009; Oyamada et al., 2020; Shirai et al., 2012, 2018).

c) Consequences of vection

The presence of vection perception may itself influence behaviour and cognition. For instance, vection is associated with postural adjustments of the head and body (Becker-Bense et al., 2012; Fushiki et al., 2005; Querner et al., 2002; Thurrell & Bronstein, 2002). Moreover, vection perception has been found to modulate the processing of vestibular stimulation (Gallagher et al., 2019), representations of peripersonal space (Kuroda & Teramoto, 2021), random number generation (Seno, Taya, et al., 2011), mental time travel (Miles et al., 2010), and memory-related emotional processing (Seno et al., 2013; Väljamäe & Seno, 2016). Further, it has been argued that vection is a necessary prerequisite for visually-induced motion sickness (VIMS; Keshavarz et al., 2015). Lastly, vection is associated with improved perspective switching, navigation, and spatial orientation in virtual reality (VR) environments, and facilitating the transfer of learning from VR simulations to real life (Palmisano et al., 2015; Riecke et al., 2015).

1.2 Sensory signals for self-motion perception

Although various sensory systems contribute to our perception of self-motion, this thesis emphasises contributions from the visual and vestibular systems. The following sections briefly outline the key ways in which these systems contribute to our perception of self-motion.

a) Contributions from the visual system

As we move through the environment our self-motion causes a structured pattern of optic flow on our retinas (Gibson, 1950). This optic flow is one of the most important contributors to the perception and control of self-motion (Lappe et al., 1999; Pitzalis et al., 2013). For example, optic flow is important for postural adjustments (Warren, 1995), modulations of walking speed (Prokop et al., 1997), and collision avoidance (Lee, 1976). Moreover, optic flow contains important information about the direction of motion (i.e., heading) and the position of the eyes relative to the visual scene (Foulkes et al., 2013; Lappe et al., 1999; van den Berg, 1992). Self-motion often occurs alongside environmental object-motion, for example, when we run to catch a moving ball. Self-motion in stationary environment produces a globally consistent optic flow pattern, while independently moving objects within the environment produce local motion signals that are inconsistent with the global optic flow pattern. To separate retinal image motion into object- and self-motion components the brain engages in a process called optic flow parsing (Foulkes et al., 2013; Rushton et al., 2018; Warren & Rushton, 2009). The brain regions responsible for optic flow parsing are a matter of debate. However, there is strong evidence to suggest that optic flow parsing involves a distributed network, comprising several brain regions that have various functional properties and, thus, contribute differently to visual motion processing (Pitzalis et al., 2020). For example, the lateral occipital region (LOR), medial temporal (MT) region, intraparietal sulcus motion area/ventral intraparietal area (IPSmot/VIP), area V6, and area V3a have all been linked to optic flow processing (Pitzalis et al., 2020). Yet, they also exhibit different functional roles, with some areas responding to heading direction (MT and VIP), while others distinguish between motion types (V6 and VIP) or are involved in the integration of multisensory visual and vestibular cues (VIP) (Pitzalis et al., 2020).

b) Contributions from the vestibular system

In contrast to the perceptual dominance of our visual system, the importance of our vestibular system is typically unknown to us unless a pathological dysfunction occurs (Dieterich & Brandt, 2008). Yet, our vestibular system contributes signals that are vital to oculomotor and postural reflexes, as well as higher cognitive functions like multisensory motion perception, attention, spatial memory and navigation, verticality perception, and bodily self-consciousness (Berthoz, 1996; Blanke et al., 2002; Brandt et al., 2014; Dieterich & Brandt, 2008; Lopez, 2013; Lopez et al., 2007).

The peripheral vestibular end organs are contained within the so-called membranous labyrinth of the inner ears, located in the temporal bone. The membranous labyrinth comprises three semicircular canals (anterior, posterior, and horizontal), along with the utricle and saccule that together form the otolith organs. The semicircular canals detect rotational accelerations, while the otolith organs detect linear accelerations, including the orientation of the head relative to gravity. Signals from the peripheral vestibular end organs are conveyed by the vestibular nerve to the vestibular nuclei in the brainstem (Khan & Chang, 2013). At this point, vestibular processing becomes multisensory as second-order neurons in the vestibular nuclei integrate vestibular signals with input from other sensory modalities (Kirsch et al., 2016). Vestibular-related signals are then relayed from the vestibular nuclei to the upper brain stem, thalamus, cerebellum, hippocampus, basal ganglia, and cortex via multiple pathways and feedback loops (Dieterich & Brandt, 2015; Hitier et al., 2014; Khan & Chang, 2013; Kirsch et al., 2016; Lopez & Blanke, 2011). The so-called 'vestibular cortex' in humans comprises a distributed network of brain areas that receive input from the vestibular system, including all multisensory cortical areas that are influenced by vestibular signals (Lopez et al., 2012; Lopez & Blanke, 2011). This includes the parieto-insular vestibular cortex (PIVC)/posterior insular region, superior temporal gyrus, inferior parietal lobule (angular and supramarginal gyrus), somatosensory cortex, precuneus, cingulate gyrus, frontal cortex (e.g., motor cortex, frontal eye fields (FEF), and the hippocampal and parahippocampal regions (Dieterich & Brandt, 2015; Khan & Chang, 2013; Kirsch et al., 2016; Lopez & Blanke, 2011; zu Eulenburg et al., 2012). In contrast to other sensory modalities, there appears to be no distinct, unimodal primary vestibular cortex (Brandt, 2003). However, it is argued that the PIVC, located in the posterior parietal operculum/retroinsular region, is the core hub of the vestibular cortical network (Brandt, 2003; Dieterich & Brandt, 2018; Kirsch et al., 2016; Lopez et al., 2012; zu Eulenburg et al., 2012).

1.3 Handedness and the lateralization of vestibular structures and functions

The cortical vestibular system exhibits a structural and functional lateralization, with a dominance of the right hemisphere in right-handers and the left hemisphere in left-handers (Dieterich & Brandt, 2018). For instance, studies combining functional neuroimaging and vestibular stimulation have consistently shown that right-handers exhibit dominant activity in the right hemisphere, particularly in the posterior insula, retroinsular area, and Sylvian fissure (Bense et al., 2003; Dieterich et al., 2003; Fink et al., 2003; Frank et al., 2016; Lopez & Blanke, 2011). This right hemisphere dominance in right-handers is also supported by evidence from vestibular neuroimaging meta-analyses (Lopez et al., 2012; zu Eulenburg et al., 2012). In left-handers, vestibular activity is observed in similar regions but with a dominance of the left hemisphere (Dieterich et al., 2003; Janzen et al., 2008), with some evidence suggesting that the lateralization of cortical vestibular processing is stronger in left-handers (Nigmatullina et al., 2016). Further, structural and connectivity mapping studies indicate that the lateralization of vestibular function is not restricted to cortical regions, but instead increases along the ascending vestibular pathways, with right-handers showing a right-sided dominance beginning in the upper brain stem and thalamus (Dieterich et al., 2017; Kirsch et al., 2016). The reciprocal organisation of handedness and vestibular function is thought to reflect a functional separation between two different spatial coordinate systems: a) a handedness coordinate system, which involves the egocentric manipulation of objects, and b) a spatial orientation coordinate system, which involves the allocentric localization of the self in the environment (Brandt & Dieterich, 2018; Dieterich & Brandt, 2018). Importantly, lateralization of vestibular function has clinical implications, as damage to the vestibular dominant hemisphere tends to produce more frequent and severe disorders of higher multisensory function, including for example hemispatial neglect and pusher syndrome (Dieterich & Brandt, 2018).

1.4 Vection in the brain: findings from PET and fMRI studies

Neuroimaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have reported links between vection perception and activity in several cortical and subcortical brain areas. As is illustrated in Table 1, these studies implement very different experimental designs, which may partially explain why their findings are not always congruent. For instance, the studies vary with regard to the plane/axis of induced vection, the use of fixation, and the measurement of vection. The studies also rely on very small sample sizes and do not always measure vection perception concurrently with neuroimaging. The brain areas that exhibit vection-related activity according to these studies are outlined in Table 2. As Table 2 demonstrates, vection perception does not locate to a single brain area or subset of brain areas, but rather involves activity dispersed across a large network. Indeed, a review of the literature has proposed a so-called probable cortical vection network, comprising visual area V3, motion area V6, area MT+ and the superior middle temporal area (MST), the ventral intraparietal area (VIP), the parieto-insular vestibular cortex (PIVC), and the cingulate sulcus visual area (CSv) (Berti & Keshavarz, 2021). In line with the fact that optic flow is the primary driver of vection, this proposed vection network overlaps substantially with a proposed cortical optic flow parsing network (Pitzalis et al., 2020). According to this latter network, the anterior precuneus (PEc), posterior cingulate area (pCi), cingulate sulcus visual area (CSv), cingulate motor area (CMA), parietal insular cortex (PIC), and the lateral occipital region (LOR) all show a preference for self-motion stimulation (Pitzalis et al., 2020). Moreover, the CSv area, CMA, PIC, and LOR not only prefer self-motion stimulation but also respond negatively to object-motion (Pitzalis et al., 2020).

Table 1. Summary of key experimental details in previous PET and fMRI studies of vection.
This table highlights the variability in experimental design across studies of vection, which is likely a contributing factor to incongruent findings in the literature. For instance, most studies use different combinations of stimulation contrasts (Stimuli/Stimulation type) and different measures for assessing vection (Vection measure). Moreover, in several studies vection is not measured for all participants (N) or is measured separately from the neuroimaging acquisition (Vection measured concurrently), making it difficult to attribute neuroimaging findings to vection perception. Furthermore, most studies included very few participants (N). Note: VAS = Visual Analog Scale; *Participants reported self-motion perception but not vection.

Author, (year)	Method	N	Stimuli	Stimulation type	Fixation	Vection measure	Stimulation duration	Vection measured concurrently
Brandt, (1998)	PET	10	Dots	- Roll - Random - Solid background	Yes	Intensity (1 - 5)	> 30 sec	Yes
Previc, (2000)	PET	9	Texture pattern	- Roll - Incoherent - Centre-field roll - Static	Yes + task	Intensity (0 – 5)	60 sec	Yes
Beer, (2002)	PET	Exp. one: 9 Exp. two/three: 6	Squares	- Coherent roll, yaw, or forward/backward - Centre-field roll - Incoherent roll, yaw, or forward/backward	Yes + task	Strength (0 – 5)	60 sec	Yes
Kleinschmidt, (2002)	fMRI	8	Windmill pattern	- Roll	Unclear	Button press for object-/ self-motion	~ 8 min	Yes
Deutschländer, (2004)	PET	Imaging: 11 Behaviour: 7	Dots	- Roll - Forward - Static	Yes	Intensity (0 – 5)	> 50 sec	No
Slobounov, (2006)	fMRI	12	Virtual reality room	- Forward/backward motion with whole/parts of room moving - Oscillations - Lateral motion -Static	Unclear	Intensity (1 – 7)	30 sec	Yes
Kovács, (2007)	fMRI	10	Spheres	- Forward - Random - Static	Yes	Prompted button press indicating object-/self-motion	60 sec coherent, 15 sec incoherent, 15 sec static	Yes
van der Hoorn, (2010)	fMRI	Imaging: 15 Behaviour:10	Dot cloud with horizon	- Forward - Backward - Wide/narrow field of view - Static	Yes	Informal report Strength (0 – 10)	6 – 12 sec	Yes & No

Becker-Bense, (2012)	PET	14	Dots	- Roll - Random - Rest	No	Intensity (0 – 10) Direction Duration	22 min	Yes
Pitzalis, (2013)	fMRI	Imaging: 13 Behaviour: 15	3-D star field	- Forward/backward - Translation - Roll - Spiral - Static - Black background with fixation	Yes	VAS: Intensity (0 – 10)	3 sec (direction reversal every 50ms)	No
Arnoldnussen, (2013)*	fMRI	Imaging: 12 Behaviour: 5	Dot cloud	- Forward - Spiral - Forward + noise - Spiral + noise	Yes	Saliency of self-/object-motion (1 – 5)	6 sec	n/a
Uesaki, (2015)	fMRI	3	Dot cloud	- Forward/backward spiral - Random (speed gradient)	Yes	Button press for object-/self-motion	16 sec	Yes
Wada, (2016)	fMRI	Imaging: 13 Behaviour: 9	Dot cloud	- Forward - Random - Static	Yes	Magnitude estimation: Strength (0 – 10)	3 sec	No
Kirollos, (2017)	fMRI	8	Star field	- Forward - Forward + oscillation - Scrambled forward - Scrambled forward + oscillation	Yes	Hold button for vection duration Magnitude estimation: Strength (0 – 100)	20 sec	Yes
Pitzalis, (2020)	fMRI	14	Naturalistic train movies	- Pure object-motion - Pure self-motion - Joint self-/object-motion - Disjoint self-/object-motion - Static	No + task	VAS: Intensity of self- & object-motion (0 – 10)	3 sec	No

Table 2. Summary of brain areas linked to vection perception by PET and fMRI vection studies. The leftmost column comprises the identified brain areas, the middle column comprises the key findings relative to the respective brain region(s), and the rightmost column comprises the motion stimulation contrast or type of vection that resulted in each finding. Note that this table includes only vection-specific findings and not findings related to general motion processing (i.e., vection-compatible stimulus vs. static imagery).

VISUAL AND VISUAL ASSOCIATION AREAS		
V1/BA 17/ Cuneus	- Shows deactivation during vection-compatible motion (Beer, 2002)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)
	- Stronger response to wide-field stimulation (Beer, 2002)	Wide-field roll vs. centre-field roll
	- Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004)	Linear vs. roll
	- **[BA 18/19/cuneus]** Activity correlates positively with vection intensity (Becker-Bense, 2012)	Roll vection
V2/ BA18	- Increased & decreased activity during vection-compatible motion (Brandt, 1998)	CW/CCW roll vs. random
	- Greater activation for vection-compatible motion (Previc, 2000)	Coherent vs. incoherent roll
	- Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004)	Roll vs. linear
	- **[BA 18/19]** Activity correlates positively with vection intensity (Brandt, 1998)	Roll vection
V3/V3a	- Greater activation for object-motion vs. vection (Kleinschmidt, 2002)	Roll vection, perceptual difference
	- Shows preference for object-motion (Arnoldussen, 2013)	Forward vs. forward + noise
	- Responds equally well to egomotion-compatible and incoherent motion (Pitzalis, 2013)	Coherent vs. incoherent
	- Responds to complex (object- and self-) motion, with no preference for object- or self-motion (Pitzalis, 2020)	Self- vs. object- vs. complex motion
V4	- Greater activation for object-motion vs. vection (Kleinschmidt, 2002)	Roll vection, perceptual difference
MT+ complex **V5/MT/MST BA 19/ Lingual gyrus**	- Increased & decreased activity during vection-compatible motion (Brandt, 1998)	CW/CCW Roll vs. random
	- Transient activation during perceptual switching & greater activation for object-motion vs. vection (Kleinschmidt, 2002)	Roll vection, perceptual difference
	- Stronger response to wide-field stimulation (Beer, 2002)	Wide-field roll vs. centre-field roll
	- **[V5/MT]** Deactivation during vection-compatible coherent yaw motion (Beer, 2002)	Coherent vs. incoherent yaw
	- Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004)	Roll vs. linear
	- **[MT+]** Greater activation for vection vs. object-motion perception (Kovács, 2007)	Forward vection, perceptual difference
	- Greater activation for forward vection-compatible vs. backward vection-compatible motion (van der Hoorn, 2010)	Forward vs. Backward
	- Shows preference for object-motion (Arnoldussen, 2013)	Forward spiral/translation vs. noise
	- **[MT]** Responds equally well to egomotion-compatible and incoherent motion (Pitzalis, 2013)	Coherent vs. incoherent
	- **[MST+]** Shows preference for egomotion-consistent stimulation (Pitzalis, 2013)	Coherent vs. incoherent

	- **[MST+]** Distinguishes types of coherent egomotion-compatible stimulation, with preference for translation and radial vs. roll motion (Pitzalis, 2013) - Greater activation during vection vs. non-vection (Uesaki, 2015) - Activity correlates positively with vection strength (Wada, 2016) - **[MT]** Shows preference for object-motion (Pitzalis, 2020) - **[MST+]** Responds to complex (object- and self-) motion, with no preference for object- or self-motion (Pitzalis, 2020) - **[BA 18/19/Lingual gyrus]** Enhanced activity during vection-compatible motion (Becker-Bense, 2012) - **[BA 19]**Activity correlates positively with vection duration (Becker-Bense, 2012)	Radial, roll, translation, spiral Forward spiral//random vection, perceptual difference Forward vection Self- vs. object- vs. complex motion Self- vs. object- vs. complex Roll vs. random Roll vection
V6	- Activity decreases as self-motion degrades (Arnoldussen, 2013) - Shows preference for egomotion-compatible stimulation (Pitzalis, 2013) - Distinguishes types of egomotion-compatible stimulation (Pitzalis, 2013) - Greater activation during vection vs. non-vection (Uesaki, 2015) - Activity correlates positively with vection strength (Wada, 2016) - Selective to optic flow but not self-motion (Wada, 2016) - Responds to complex (object- and self-) motion, with no preference for object- or self-motion (Pitzalis, 2020)	Forward spiral Coherent vs. incoherent motion Radial, roll, translational, spiral Spiral/random forward vection, perceptual difference Forward vection Forward vs. incoherent/static Self- vs. object- vs. complex motion
LOR	- Shows preference for self-motion & responds negatively to object-motion (Pitzalis, 2020)	Self- vs. object- vs. complex motion
KO/ occipital pole	- Greater activation during vection-compatible motion (Beer, 2002) - Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear) Roll vs. linear
CINGULATE AREAS		
CSv	- Activity decreases as self-motion degrades (Arnoldussen, 2013) - Selective to self-motion direction (Arnoldussen, 2013) - Weakly activated by egomotion-compatible stimulation & inhibited by random motion/static images (Pitzalis, 2013) - Does not distinguish types of coherent motion (Pitzalis, 2013) - Activity correlates positively with vection strength (Wada, 2016) - Selective to coherent, vection-compatible motion (Wada, 2016) - Greater response to oscillating vection-compatible vs. smooth vection-compatible motion (Kirollos, 2017) - Greater activation during global vection-compatible vs. scrambled motion (Kirollos, 2017)	Forward spiral Forward translation vs. forward spiral Coherent vs. incoherent motion vs. static Forward/backward vs. roll vs. translation vs. spiral Forward vection Forward vs. incoherent/static Forward smooth vs. forward oscillating Global forward vs. scrambled forward motion

	- Shows preference for self-motion & responds negatively to object-motion (Pitzalis, 2020)	Self- vs. object- vs. complex motion
Anterior cingulate	- Decreased activity during vection-compatible motion (Brandt, 1998)	CW roll vs. random
	- Activity correlates positively with vection intensity (Brandt, 1998)	CCW roll vection
	- Greater activity during vection-compatible coherent motion (Beer, 2002)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)
	- Greater activation during vection vs. object-motion (Kovács, 2007)	Forward vection, perceptual difference
	- Enhanced activity during vection-compatible motion (Becker-Bense, 2012)	Roll vs. random
	- **[BA 24/31/32]** Activity correlates positively with vection intensity (Becker-Bense, 2012)	Roll vection
Posterior cingulate/ BA 31	- Greater activity during vection-compatible motion (Brandt, 1998)	Roll vs. random
	- Activity correlates positively with vection intensity (Brandt, 1998)	CW/CCW roll vection
CMA	- Prefers self-motion & responds negatively to object-motion (Pitzalis, 2020)	Self- vs. object- vs. complex motion
Cingulate	- Greater activation during vection-compatible coherent motion (Beer, 2002)	Coherent yaw/linear vs. incoherent yaw/linear
PARIETAL AREAS		
VIP/IPS(mot)/ LIP	- Greater activation during vection vs. object-motion (Kovács, 2007)	Forward vection, perceptual difference
	- Selective to self-motion direction (Arnoldussen, 2013)	Forward vs. forward spiral
	- Greater activation during vection vs. non-vection (Uesaki, 2015)	Forward spiral/random vection, perceptual difference
	- Shows preference for egomotion-compatible stimulation (Pitzalis, 2013)	Coherent vs. incoherent
	- Distinguishes between types of egomotion-compatible stimulation (Pitzalis, 2013)	Linear vs. roll vs. translation vs. spiral
	- Responds to complex (object- and self-) motion, with no preference for object- or self-motion (Pitzalis, 2020)	Self- vs. object- vs. complex motion
Precuneus **PcM/pCi/ BA 7/PEc/ Superior parietal lobule**	- Greater activation during vection-compatible motion (Brandt, 1998)	Roll vs. random
	- **[BA7]** Activity correlates positively with vection intensity (Brandt, 1998)	CCW roll vection
	- Greater activation for vection-compatible roll vs. vection-compatible linear motion (Deutschländer, 2004)	Roll vs. linear
	- Greater activation during vection vs. object-motion (Kovács, 2007)	Forward vection, perceptual difference
	- Enhanced activity during vection-compatible motion (Becker-Bense, 2012)	Roll vs. random
	- **[BA40/39]** Activity correlates positively with vection intensity (Becker-Bense, 2012)	Roll vection
	- Activity correlates positively vection strength (Wada, 2016)	Forward vection
	- Selective to coherent, vection-compatible motion (Wada, 2016)	Forward vs. incoherent/static
	- **[pCi & PEc]** Shows preference for self-motion (Pitzalis, 2020)	Self- vs. object-vs. complex motion

Parietal lobe/ BA 39/ BA 40/ supramarginal/ Angular gyrus	- Responds differently to CW and CCW vection-compatible roll (Previc, 2000) - Greater activation for vection-compatible roll vs. vection-compatible linear motion (Deutschländer, 2004)	CW vs. CCW roll Roll vs. linear
Medial parieto-occipital cortex	- Transient activation during perceptual switching (Kleinschmidt, 2002)	Roll vection, perceptual difference
TEMPORAL & INSULAR AREAS		
PIVC/PIC	- Greater deactivation during vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004) - Greater deactivation during vection vs. object-motion (Kleinschmidt, 2002) - Greater activation during vection vs. non-vection (Uesaki, 2015) - Activity correlates positively with vection strength (Wada, 2016) - Stronger response to oscillating vection-compatible vs. smooth vection-compatible motion (Kirollos, 2017) - **[PIC]** Shows preference for self-motion & responds negatively to object-motion (Pitzalis, 2020)	Roll vs. linear Roll vection, perceptual difference Forward spiral/random vection, perceptual difference Forward vection Forward smooth vs. forward oscillating Self- vs. object- vs. complex motion
Insula/ retroinsular cortex	- Decreased activation during vection-compatible motion (Brandt, 1998) - Greater activation for vection-compatible motion (or inhibition for incoherent motion) (Previc, 2000) - Greater activation for vection-compatible roll motion (Beer, 2002) - Responds differently to vection-compatible linear vs. vection-compatible roll motion, with stronger deactivation during linear motion (Deutschländer, 2004)	Roll vs. random Roll vs. incoherent Roll vs. incoherent Roll vs. linear
Fusiform gyrus/ BA 37/ Inferior temporal area	- Decreased activation during vection-compatible motion (Brandt, 1998) - Greater activation for vection-compatible motion (or inhibition for incoherent motion) (Previc, 2000) - Greater activity during vection-compatible motion (Beer, 2002) - Greater activation during vection-compatible forward motion vs. vection-compatible backward motion (van der Hoorn, 2010)	CW roll vs. random Roll vs. incoherent Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear) Forward vs. Backward
Superior temporal gyrus/ BA 22/42	- Decreased activity during vection-compatible motion (Brandt, 1998) - Greater activation for vection-compatible motion (or inhibition for incoherent motion) (Previc, 2000) - Greater activation for vection-compatible roll vs. vection-compatible linear motion (Deutschländer, 2004) - **[superior/middle temporal area]** Activity correlates positively with vection duration (Becker-Bense, 2012)	CW roll vs. random Roll vs. incoherent Roll vs. linear Roll vection
PRE-/POST-CENTRAL AREAS		
Precentral gyrus	- Greater activation during vection vs. object-motion (Kovács, 2007)	Forward vection, perceptual difference

Central/postcentral BA3/5/ BA 21/12	- Enhanced activity during vection-compatible motion (Becker-Bense, 2012)	Roll vs. random
p2v	- Selective to self-motion direction (Arnoldussen, 2013)	Forward vs. forward spiral
FRONTAL AREAS		
Inferior frontal gyrus/BA 44	- Activation difference for CW vs. CCW vection-compatible roll (Previc, 2000) - Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschlander, 2004) - Activity correlates positively with vection intensity (Becker-Bense, 2012)	CW vs. CCW roll Roll vs. linear Roll vection
Middle/superior frontal gyrus BA 46/ BA 10	- Increased & decreased activity during vection-compatible motion (Brandt, 1998) - Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschlander, 2004) - Activity correlates positively with vection duration (Becker-Bense, 2012)	Roll vs. random Roll vs. linear Roll vection
SFS/FEF/ Medial frontal gyrus/ BA 8/ BA 9/ BA 6	- Greater activation during vection vs. object-motion (Kovács, 2007) - Enhanced activity during vection-compatible motion (Becker-Bense, 2012) - Activity correlates positively with vection (Becker-Bense, 2012) - Responds to complex (object- and self-) motion, with preference for self-motion (Pitzalis, 2020)	Forward vection, perceptual difference Roll vs. random Roll vection Self- vs. object- vs. complex motion
THALAMUS/PULVINAR		
	- Decreased activation during vection-compatible motion (Brandt, 1998) - Greater activity during vection-compatible motion (Beer, 2002)	CW roll vs. random Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)
HIPPOCAMPAL AREAS		
Parahippocampal gyrus/ PPA/ BA 30/ BA 28	- Increases & decreases in activity during vection compatible motion (Brandt, 1998) - Responds differently to CW vs. CCW vection-compatible roll (Previc, 2000) - Stronger response to wide-field stimulation (Beer, 2002) - Responds differently to vection-compatible linear vs. vection-compatible roll motion (Deutschländer, 2004) - Activity correlates positively with vection duration (Becker-Bense, 2012) - **[PPA]** Responds to complex (object- and self-) motion, with no preference for object- or self-motion (Pitzalis, 2020)	CW roll vs. random CW vs. CCW roll Wide-field vs. centre-field CCW roll Roll vs. linear Roll vection Self- vs. object- vs. complex motion
AMYGDALA		
	- Greater activation during vection-compatible coherent motion (Beer, 2002)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)

BASAL GANGLIA		
Putamen/ caudate nucleus	- Greater activation for vection-compatible motion (or inhibition for incoherent motion) (Previc, 2000)	Roll vs. incoherent
	- Responds differently to CW vs. CCW vection-compatible roll (Previc, 2000)	CW vs. CCW roll
	- Greater activation for vection-compatible motion (Beer, 2002)	Roll vs. incoherent roll
	- Greater activation during vection vs. object-motion (Kovács, 2007)	Forward vection, perceptual difference
BRAINSTEM		
Midbrain/Pons	- Greater activation during vection-compatible motion (Brandt, 1998)	CCW roll vs. random
	- Responds differently to CW vs. CCW vection-compatible roll (Previc, 2000)	CW vs. CCW coherent roll
	- Greater activity during vection-compatible motion (Beer, 2002)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)
CEREBELLUM		
	- Greater activation for vection-compatible motion (Previc, 2000)	Roll vs. incoherent
	- Greater activation during vection vs. object-motion (Kleinschmidt, 2002)	Roll vection, perceptual difference
	- Deactivation during vection-compatible motion (Beer, 2002)	Coherent (roll/yaw/linear) vs. incoherent (roll/yaw/linear)
	- **[Vermis]** Enhanced activity during vection-compatible motion (Becker-Bense, 2012)	Roll vs. random
	- **[Vermis/parahippocampal gyrus]** Activity correlates positively with vection (Becker-Bense, 2012)	Roll vection

BA = Brodmann area; CMA = cingulate motor area; CSv = cingulate sulcus visual area ; FEF = frontal eye fields; IPS = intraparietal sulcus; IPSmot = intraparietal sulcus motion area; KO = kinetic occipital region; LIP = lateral intraparietal region; LOR = lateral occipital region; MST = medial superior temporal area; MT = middle temporal visual area; pCi = posterior cingulate area; PcM = precuneus motion area; PEc = part of the anterior precuneus; PIC = parietal insular cotex; PIVC = parieto-insular vestibular cortex; PPA = parahippocampal place area; p2v =putative 2v area (dorsal postcentral sulcus); SFS = superior frontal sulcus region; VIP = ventral intraparietal area
Perceptual difference = periods of object- vs. self-motion perception

a) Reciprocal inhibitory visual-vestibular interaction as a mechanism for self-motion perception

Several early neuroimaging studies observed *activation* of primary and secondary visual cortices with concurrent *deactivation* of multisensory vestibular cortex – primarily the PIVC - during vection-inducing stimulation (Brandt et al., 1998; Deutschländer et al., 2004; Kleinschmidt et al., 2002). This activation-deactivation pattern is thought to reflect a mechanism of reciprocal inhibitory visual-vestibular interaction for self-motion perception, in which the dominant sensorial weight is shifted from one sensory modality to the other in order to protect self-motion perception from sensory mismatches and avoid perceptual ambiguity (Brandt et al., 1998, 2002, 2003; Brandt, 2003). In the case of vection, this mechanism protects visually driven self-motion perception against conflicting or mismatched vestibular inputs by functionally down-regulating vestibular sensitivity, resulting in deactivation of the PIVC. Conversely, vestibular stimulation – which invariably signals self-motion - leads to deactivation of visual cortex (Bense et al., 2001; Deutschländer et al., 2002; Wenzel et al., 1996).

Although this activation-deactivation pattern is associated with vection, visual-vestibular interactions are complex and the mere presence of this activity pattern is neither responsible for, nor indicative of vection perception. For instance, similar activation-deactivation patterns have been reported in visual and vestibular networks in the absence of vection (Becker-Bense et al., 2012; Deutschländer et al., 2004; Previc et al., 2000). Moreover, some evidence points to vection-related *activation*, rather than deactivation, of the posterior insular cortex/PIVC (Kirollos et al., 2017; Uesaki & Ashida, 2015). Lastly, the posterior insular cortex/PIVC region exhibits a vection-independent preference for coherent and egomotion-compatible stimulation (Antal et al., 2008; Cardin & Smith, 2010), but does not appear to distinguish between types of coherent motion (Antal et al., 2008). Altogether, this suggests that the posterior insular cortex/PIVC is sensitive to coherent visual motion stimulation rather than vection per se.

The incongruence of the evidence linking vection perception and activity in the posterior insular cortex/PIVC is likely exacerbated by two factors. Firstly, there is now evidence to suggest that there are two distinct motion regions along the human posterior insula: a) the PIVC, which shows activation during vestibular stimulation and suppression during visual stimulation, and b) the posteriorly located PIC, which is multisensory and shows activations during both visual and vestibular stimulation (Frank et al., 2016; Greenlee et al., 2016). As these adjacent regions are undifferentiated in many studies, the mixed findings in the posterior insular cortex likely reflect the different functional properties of these regions in relation to both vection and visual motion processing. Secondly, differences in the amount of visual-vestibular conflict induced in various studies may result in different posterior insular cortex/PIVC (de)activation patterns (Kirollos et al., 2017; Nishiike et al., 2002; Uesaki & Ashida, 2015). For example, deactivations in this region are typically reported in studies that simulate smooth, constant velocity self-motion (e.g., Brandt et al., 2002; Deutschländer et al., 2004; Kleinschmidt et al., 2002). If this optic flow resulted from actual motion, one would expect minimal, transient vestibular signals (e.g. at motion onset). Thus, such studies induce a low-conflict visual-vestibular interaction. In contrast, studies reporting activation of this region often simulate complex self-motion, with changes in speed and heading (e.g., Kirollos et al., 2017; Uesaki & Ashida, 2015). If this optic flow resulted from actual motion, one would expect accompanying sustained and dynamic vestibular signals. Thus, such studies induce a high-conflict visual-vestibular interaction.

1.5 Studying vection: methodological limitations and potential solutions

Much of our knowledge about the neural mechanisms of vection perception derives from PET and fMRI studies. Yet, like all neuroimaging techniques, these methods have several limitations that constrain the empirical questions we can ask. Although these methods offer high spatial resolution, their relatively poor temporal resolution means that they likely fail to capture dynamic, time-sensitive vection activity in the brain. Indeed, the sluggish nature of PET and fMRI signals means that findings based on these methods likely represent an amalgamation of vection-related activity, rather than time-sensitive vection dynamics such as onset, offset, or maintenance. Moreover, the inability to accurately track the temporal dynamics of vection might mean that these methods are unsuited to questions about subjective variability in, for example, onset latency.

These methods also have physical constraints that are particularly limiting in vection research. Firstly, the size of the scanning bore means that visual motion stimulation is typically constrained to near-space, small-field presentations. There is strong evidence showing that large-field stimulation generates compelling vection whereas small-field stimulation produces comparatively weaker vection (Beer et al., 2002; Brandt et al., 1973; Keshavarz et al., 2017; Previc et al., 2000). Thus, the physical constraints of these methods likely limit the quality of vection that can be experienced and studied. Moreover, these methods require participants to lie supine, which itself alters the visual-vestibular conflict with respect to the gravity vector. Indeed, an EEG study that exposed participants to the same visual stimulation in upright and supine positions found differences in vection-specific brain activity between the two positions, which are thought to reflect visual-vestibular conflict differences between the two positions (Harquel et al., 2020). Further, participants reported comparable vection frequency and duration but different bodily sensations in the two positions (Harquel et al., 2020).

With regard to fMRI, there is now strong evidence for so-called magnetic vestibular stimulation (MVS), in which the magnetic field in an MRI scanner stimulates the vestibular system, resulting in transient sensations of vertigo, dizziness, or motion (Boegle et al., 2016; Ward et al., 2015). Although an individual's perception of vertigo and motion may abate over their time inside the MRI machine, the vestibular stimulation persists (Ward et al., 2015) and may result in activity modulations in brain regions associated with vestibular and oculomotor functions (Boegle et al., 2016). Thus, fMRI studies of vection must be carefully designed to ensure that effects obtained in the multisensory vestibular network are appropriately attributed to vection.

One method that circumvents many of the limitations of PET and fMRI and that may prove particularly useful in vection research is electroencephalography (EEG). EEG provides an online, temporally precise measure of brain activity making it well suited for investigating the relationship between continuous changes in brain activity and the time course of vection perception. Further, the portability of EEG means that it can easily be employed in various experimental settings. This means that vection-inducing stimuli need not be constrained to a computer screen, but can instead be presented in the form of large-projections, virtual environments, and even combined with actual motion using motion platforms or immersive (e.g. flight) simulators. Lastly, as EEG has few physical constraints, it can also be used to compare vection-related brain activity across different head and body positions (e.g., supine, upright, standing, head tilt).

a) Fundamentals of EEG

Electroencephalography (EEG) involves the recording of neurophysiological activity using multiple electrodes placed along the scalp surface. The EEG signal provides a direct measure of neural activity, reflecting a summation of excitatory and inhibitory postsynaptic potentials at the dendrites of neuronal ensembles with parallel geometric orientations (Cohen, 2014). When neurotransmitters activate cell membrane ion channels, bidirectional ion flow begins between the neuron and extracellular space, changing the potential and producing an electrical field around the neuron (Cohen, 2014). For electrical fields to be large enough to be visible at the scalp, a large number of neurons (estimated to be around 10^7) with a similar geometric orientation must be simultaneously active (Woodman, 2010). It is widely believed that the postsynaptic activity in populations of cortical pyramidal cells is the primary source of the EEG signal (Jackson & Bolger, 2014; Woodman, 2010). Importantly, the high temporal resolution of EEG allows us to capture cognitive dynamics in the time frame in which they occur, i.e., tens to hundreds of milliseconds (Cohen, 2014).

This thesis focuses on two aspects of the EEG signal in relation to the processing of vection-inducing motion stimulation: a) event-related potentials (ERPs) and b) neural oscillations. ERPs are time-locked, average EEG activations that occur in response to sensory, cognitive, or motor events. In other words, ERPs are the averaged voltage deflections that are observed prior to, or in response to a given event. The ERP waveform comprises several component waves, each defined by polarity, timing, scalp distribution, and sensitivity to experimental manipulation (Woodman, 2010). Although component nomenclature varies between studies, there is consistent evidence linking particular components and cognitive processes. For example, the P1 component is thought to index sensory and perceptual processing whereas the N2 is typically associated with object recognition and categorisation (Woodman, 2010). Neural oscillations refer to the rhythmic fluctuations in the excitability of neuronal populations and are typically characterised by their frequency, amplitude, phase, coherency, and topography (Cohen, 2014). In humans, observable EEG oscillations are commonly categorised into the following (approximate) frequency bands: delta (1 – 4 Hz), theta (4 – 8 Hz), alpha (8 – 12 Hz), beta (13 – 30 Hz), and gamma (30 – 100 Hz). A wide range of cognitive processes have been linked to the oscillatory activity in each of these frequency bands. For example: delta oscillations are associated with attentional processes; theta oscillations are associated with memory and executive functioning; alpha oscillations are associated with attention, and the suppression and selection of sensory stimuli; beta oscillations are associated with motor control; and gamma oscillations are associated with the attentive processing of information and conscious perception (Herrmann et al., 2016).

In contrast to its high temporal resolution, EEG offers relatively limited spatial resolution. Moreover, according to the so-called inverse problem, we cannot know where in the brain a distribution of electrical potential observed at the scalp was generated, unless we know the number of synchronously active generators a priori. Several algorithms, each with their own set of assumptions and constraints, have been devised to estimate the location of EEG sources. The studies in this thesis use one of the most popular algorithms - the (exact) low-resolution brain electromagnetic tomography algorithm ((e)LORETA; Pascual-Marqui, 2002; Pascual-Marqui, 2007) – to estimate the source of observed EEG activity in the brain.

1.6 Vection in the brain: findings from EEG studies

Although becoming increasingly popular, very few have studies have investigated vection perception using EEG. The following sections briefly outline the key findings from a) ERP and b) oscillation-based studies.

a) Vection and event-related potentials (ERPs)

As vection perception develops gradually and has both variable onset latency and duration, ERPs cannot be time-locked to vection onset or offset. As a result, ERP studies of vection cannot examine vection perception directly. Instead, ERPs are used to investigate a) the early processing of vection-compatible visual motion stimulation prior to vection onset or b) how the cognitive processing of other events is modulated by vection presence. The key findings from such studies are outlined below.

The N70 component

One of the earliest vection studies to investigate ERPs employed a central, pattern-reversing checkerboard with a moving surround that generated alternating periods of vection and object-motion perception (Thilo et al., 2003). The study found reduced occipital N70 amplitudes in response to the central target during periods of vection perception (Thilo et al., 2003). As the visual stimulation was identical during periods of vection and object-motion perception, the observed reduction in occipital N70 amplitude is thought to reflect a top-down reduction of primary visual cortex excitability due to self-motion processing (Thilo et al., 2003). The idea that self-motion perception modulates early visual processing is also supported by PET and fMRI studies showing deactivation of early visual cortex during vection-inducing stimulation (Brandt et al., 1998; Kleinschmidt et al., 2002).

The P1/P2 components

Studies comparing the ERPs evoked by the motion onset of various centre-periphery motion patterns suggest that parieto-occipital P1/P2 components index the early processing of visual motion stimulation and potentially the detection of conflicting or incoherent motion (Berti et al., 2019; Keshavarz & Berti, 2014). Although the P1/P2 components reflect visual motion processing several seconds prior to vection onset, there is some evidence to indicate that these components may partly index vection-related processes. For instance, when participants were exposed to the same motion patterns for a prolonged period in a separate session, it was revealed that the patterns that evoked the smallest P1/P2 components also generated the weakest vection (Berti et al., 2019; Keshavarz & Berti, 2014).

The N2 component

Evidence from several studies suggests a tentative relationship between parieto-occipital N2 component amplitude and the subjective perception of vection strength/intensity (Berti et al., 2019; Keshavarz & Berti, 2014; Wei et al., 2019). Given that the N2 component in these studies is time-locked to motion onset, which typically occurs several seconds prior to vection onset, it cannot be considered a correlate of vection per se. Rather, the N2 component likely indexes aspects of early visual motion processing which are important for later vection perception (e.g. motion coherency).

The P3 and P400 components

Studies examining the potential influence of vection perception on simultaneous cognitive task performance have identified vection-related modulations of late, task-based ERP components. For example, the P3 component in response to oddball paradigm targets has a reduced amplitude and shifted peak latency when concurrent vection-compatible stimulation is present (Strozak et al., 2016). Another study reported attenuation of P3 component amplitude during a change detection task in participants who experienced high-frequency vection, but not in participants who experienced low-frequency vection (Strozak et al., 2019), indicating that the influence of vection on cognitive task performance may be dependent on the subjective quality of the experienced vection. The same study also found an amplitude reduction and topographical shift of the N400 component during vection perception, as compared to object-motion perception (Strozak et al., 2019).

b) Vection and neural oscillations

Although investigations into the relationship between neural oscillations and vection perception are rare, such studies have consistently found evidence to link vection perception with alpha oscillations. One of the earliest EEG studies of vection found differences between vection and non-vection periods in the high alpha (10 – 12 Hz) band, but not in the theta, low alpha (8 – 9 Hz), or beta bands (Tokumaru et al., 1999). Although the study had several limitations (i.e., including only five participants and not measuring vection directly), subsequent studies have confirmed an association between vection-inducing stimulation and alpha oscillations. For example, vection-compatible motion is associated with decreased parieto-occipital alpha power (Obereisenbuchner et al., 2021) and modulation of alpha band steady state visually evoked potentials (SSVEPS) (Dowsett et al., 2020).

Moreover, emerging evidence suggests that alpha band dynamics may index specific aspects of vection perception. For instance, increased 10 Hz alpha activity following motion stimulation onset is associated with stronger vection perception, while alpha band increases after motion offset are correlated with vection intensity (Palmisano et al., 2016). Moreover, alpha power in the cortical sensorimotor network decreases around the time of vection onset, while parieto-occipital alpha power increases during ongoing vection perception in upright participants (Harquel et al., 2020). Study 1 in the present thesis also provides evidence linking alpha band changes with vection dynamics, finding that parieto-occipital alpha power decreases around vection onset but increases during ongoing vection perception (McAssey et al., 2020, see section 2.1).

Lastly, there is also some evidence to suggest that activity in other oscillation bands may be related to vection perception. For example, amplitude decreases in the delta and beta bands are negatively associated with subjective vection intensity (Palmisano et al., 2016), while stronger theta-band phase synchronisation is observed during vection-compatible, versus vection-incompatible, visual motion stimulation (Wei et al., 2019).

1.7 About this thesis

This thesis is concerned with the study of visually-induced vection perception, a phenomenon that involves reciprocal visual-vestibular interaction. Although lateralization of the cortical multisensory vestibular network is well established, with left-handers exhibiting a left-hemisphere dominance and right-handers exhibiting a right-hemisphere dominance, studies investigating vection perception in left- versus right-handers are lacking. Further, although EEG offers the opportunity to examine the relationship between continuous brain activity changes and vection perception dynamics, few such studies have been conducted. To address these gaps in the literature, this thesis aimed to study vection perception using EEG techniques and to examine the potential hemispheric lateralization of vection processing in left- and right-handers.

The first step in this doctoral work involved creating an experimental setup that could generate stable, compelling vection perception. This required the construction of a custom experimental apparatus that presented large-field visual motion stimulation onto a dome. The next step involved the design and implementation of a novel control stimulus. In contrast to the control stimuli used in previous vection studies, this control stimulus matched the low-level visual properties (e.g., luminance, global velocity, etc.) contained in the vection-inducing stimulus, but rarely produced vection perception. Through the creation of this control stimulus, the studies conducted as part of this thesis are uniquely equipped to identify vection-related brain activity while attenuating confounding effects due to stimulus differences or general motion processing.

The first study in this thesis (Chapter 2.1) investigated the behavioural characteristics and neural oscillations associated with vection perception in left- versus right-handers. Participants were exposed to vection-inducing visual motion stimulation and to the novel control stimulus while EEG was recorded. Vection perception was assessed in real time, with participants indicating vection onset, offset, and direction during the motion stimulation. Perceived vection strength was also recorded on a trial-by-trial basis. To determine if left- and right-handers experience vection differently, both groups were compared on several behavioural measures of vection, including frequency, onset latency, duration, and perceived vection strength. Fast Fourier Transform (FFT) analyses were conducted to investigate differences in theta, alpha and beta bands between the vection-compatible stimulation and the control stimulation, for both left- and right-handers. Given that alpha oscillations have previously been linked with vection (Palmisano et al., 2016; Tokumaru et al., 1999) and bistable perception (Struber & Herrmann, 2002), time-frequency analyses were conducted to investigate alpha band activity around vection onset and during ongoing vection perception, for both left- and right-handers.

The second study in this thesis (Chapter 2.2) had two major aims: 1) to investigate the temporal activation of the vection network by vection-compatible visual motion stimulation and 2) to examine the potential lateralization of these processes in left- versus right-handers. This study employed the same experimental design outlined in the first study. To investigate the temporal activation of the vection network, the ERPs evoked by vection-compatible motion were compared against those evoked by the control stimulation, for left- and right-handers respectively. Potential differences between left- and right-handers were examined by contrasting the condition difference waves (i.e., ERPs evoked by vection-compatible motion minus ERPs evoked by control motion) observed in each group. Source localization analyses (eLORETA) were conducted to estimate the brain areas involved in the observed ERP effects and to examine the potential lateralization of these effects in left- versus right-handers. While this study focused on the neural processes preceding vection perception, rather than vection per se, correlation analyses between ERP activity and behavioural measures of vection were conducted to investigate the relationship between the early processing of vection-compatible stimulation and the later subjective experience of vection.

2. CUMULATIVE-STYLE THESIS: STUDIES

This cumulative-style thesis includes two original EEG studies investigating vection processing and perception in left- and right-handers. The first study (Study 1, section 2.1) has been published in a peer-reviewed journal. The second study (Study 2, section 2.2) has been submitted for peer-reviewed publication. Both studies are presented below.

2.1 Study 1: Different EEG brain activity in right and left handers during visually-induced self-motion perception

This study has been published as:

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Author contributions:

Michaela McAssey, Marianne Dieterich, and Thomas Brandt conceived the experiment. Michaela McAssey and James Dowsett programmed the experiment. Michaela McAssey collected the data. Michaela McAssey analysed the data with the assistance of James Dowsett and Valerie Kirsch. Michaela McAssey drafted the manuscript, with feedback and revisions from Marianne Dieterich and Thomas Brandt. All authors commented on and approved the final manuscript. Michaela McAssey is the only first author of the paper.

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ORIGINAL COMMUNICATION

Different EEG brain activity in right and left handers during visually induced self-motion perception

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Abstract

Visually induced self-motion perception (vection) relies on visual–vestibular interaction. Imaging studies using vestibular stimulation have revealed a vestibular thalamo-cortical dominance in the right hemisphere in right handers and the left hemisphere in left handers. We investigated if the behavioural characteristics and neural correlates of vection differ between healthy left and right-handed individuals. 64-channel EEG was recorded while 25 right handers and 25 left handers were exposed to vection-compatible roll motion (coherent motion) and a matched, control condition (incoherent motion). Behavioural characteristics, i.e. vection presence, onset latency, duration and subjective strength, were also recorded. The behavioural characteristics of vection did not differ between left and right handers (all $p > 0.05$). Fast Fourier Transform (FFT) analysis revealed significant decreases in alpha power during vection–compatible roll motion ($p < 0.05$). The topography of this decrease was handedness-dependent, with left handers showing a left lateralized centro-parietal decrease and right handers showing a bilateral midline centro-parietal decrease. Further time–frequency analysis, time locked to vection onset, revealed a comparable decrease in alpha power around vection onset and a relative increase in alpha power during ongoing vection, for left and right handers. No effects were observed in theta and beta bands. Left and right-handed individuals show vection-related alpha power decreases at different topographical regions, possibly related to the influence of handedness-dependent vestibular dominance in the visual–vestibular interaction that facilitates visual self-motion perception. Despite this difference in where vection-related activity is observed, left and right handers demonstrate comparable perception and underlying alpha band changes during vection.

Keywords Roll vection · Self-motion perception · Visual motion perception · Thalamo-cortical vestibular dominance · Hemispherical lateralization · Right and left handers · EEG

Introduction

Self-motion perception relies on the contributions of multiple sensory systems, with the most important contributions from the visual and vestibular systems. Although vestibular stimuli invariably signal the sensation of self-motion, visual motion stimuli can produce two alternate interpretations with the observer perceiving that (a) they are stationary in a moving surround, i.e. object motion or (b) they are moving in a stationary surround, i.e. self-motion. When a stationary observer is presented with a large-field visual motion stimulation, a sensation of apparent self-motion, i.e. vection, occurs [1]. Vection highlights the important role of the visual system in self-motion perception. Indeed, while the vestibular system elicits information about body motion at acceleration and deceleration, it is visual information that

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allows us to perceive self-motion at a constant velocity (e.g. car motion).

Early positron emission tomography (PET) and functional MRI (fMRI) imaging studies have shown that optokinetic stimuli used to induce vection are associated with both activation of visual cortex and concurrent deactivation of parieto-insular vestibular cortex, PIVC [2–5]. These findings have been hypothesized to reflect an inhibitory reciprocal visual–vestibular interaction as a mechanism for self-motion perception, in which the dominant sensorial weight is shifted from one modality to the other more reliable modality [2, 6]. In terms of vection, inhibition of the vestibular cortex reflects the actual, missing vestibular input as compared to the expected vestibular input. It is important to note that the relationship between these systems is multifaceted and the observation of concurrent activation/deactivation of these systems is not itself indicative of vection presence. For example, visual motion stimulation has been shown to produce increased activity in the visual cortex and concomitant decreased activity in the PIVC even in the absence of vection [3, 7]. Furthermore, it has been demonstrated that the presence of acceleration in visual motion stimuli may lead to increased, rather than decreased, activations of the PIVC during vection [8, 9]. This modulation of the visual–vestibular interaction during visual self-motion is thought to result from selectivity of the PIVC to visual gravitational motion [10].

Distinguishing between activity that corresponds to visual motion stimulation versus that which corresponds to vection per se is a major challenge if we are to understand the neural basis of visual self-motion perception. Early studies identified large networks of regions with activations and deactivations attributed to visual self-motion perception [4, 11–14]. However, some of these studies did not directly test whether vection was experienced by participants, but rather relied on stimuli consistent with self-motion [14] or stimuli which were assumed to induce vection [11, 14], making it difficult to infer if the findings relate to visual motion stimulation or vection. Isolating vection-related neural activity is also made difficult by the fact that visual motion stimuli do not generate a continual sensation of vection, but rather tend to produce bistable perception with alternating periods of object- and self-motion perception [1, 5, 15]. Furthermore, even when vection is present, there are large differences in reported vection strength and duration between individuals [16].

The present study investigated the behavioural characteristics and neural correlates of vection in left and right handers because several PET and fMRI studies using vestibular stimulation have revealed a vestibular thalamo-cortical dominance in the right hemisphere in right handers and the left hemisphere in left handers [17–28]. EEG recordings synchronized with participants' perceptual states were obtained in order to accurately distinguish between periods of object- and self-motion. Given that alpha oscillations have been linked to vection [29–31] and associated with bistable perception [32–34], the EEG analyses focused primarily on alpha band activity and on potential differences in this band between left and right handers.

Materials and methods

Participants

A total of 25 right handed (14 females, age: 27.68 years *SD*: 4.02 years) and 25 left handed (18 females, age: 24.83 years *SD*: 4.24 years) healthy adults participated in the experiment. All participants had normal or corrected-to-normal vision and reported no prior history of vestibular symptoms or neurological disorders. Participants completed the 10-item Edinburgh Handedness Inventory to determine their handedness (right handers: $8\% > +40$, $16\% > +60$, $16\% > +70$, $8\% > +80$, $52\% > +90$; left handers: $8\% > -40$, $4\% > -50$, $24\% > -60$, $20\% > -70$, $20\% > -80$, $24\% > -90$). The experiment was conducted in accordance with the guidelines of the institutional ethics committee and the Declaration of Helsinki. All participants gave their informed written consent prior to their participation and received compensation (€10/h).

Visual motion stimulation

The stimuli comprised two movies: a coherent and an incoherent rotating pattern of dots. The stimuli were generated in MATLAB (The MathWorks Inc., Natick, MA, USA) using the Psychophysics Toolbox extensions. The stimuli consisted of 1000 randomly spaced white dots on a black background. A central green dot provided a fixation point. The dots rotated in the roll plane in either a clockwise (CW) or counter-clockwise (CCW) direction at 30°/s. In the coherent condition the dots rotated in a smooth circular formation. In contrast, the dots in the incoherent condition had a random sinusoidal movement in both the *X* and *Y* direction added to the overall circular trajectory (i.e. the phase and amplitude of the additional sinusoidal movement was randomized separately for each dot). This resulted in each individual dot appearing to follow a random trajectory, but with the global pattern maintaining either a CW or CCW direction with a mean velocity of 30°/s. The stimuli were projected onto a custom-built dome (diameter: 75 cm) apparatus with the rotation axis passing through the dome centre. The distance between the apex of the dome and the participant's nasion was 31 cm, with the visual field subtending a visual angle of 100°. The experiment was conducted in a dark room with the visual stimulus covering the participant's entire field of view, ensuring that no horizontal or vertical cues were observable.

Experimental procedure

Prior to the beginning of the experiment, the height of the dome apparatus was adjusted such that participant's line of sight was in-line with the centre of the dome. As illustrated in Fig. 1a each trial began with the presentation of stationary dots for a jittered period (range 3–5 s), followed by dot rotation (20 s) and then a return to stationary dots (10 s). Participants were instructed maintain fixation on the central green dot for the duration of the trial and to avoid following the moving dots with their eyes. During the dot rotation, participants reported vection onset and vection offset by means of a button push on a gaming controller. Separate buttons were denoted for perceived CW and perceived CCW vection onset/offset, with participants holding the controller with both hands and making responses with both index and middle fingers. At the end of each trial, participants were asked to verbally report on the strength of their vection experience on a scale of 0 ('no vection') to 10 ('I felt I was really moving'). This response was recorded by the experimenter before the next trial begun. Participants were seated with their head on a chin rest during each trial. The experiment comprised a total of 100 trials: 50 coherent trials and 50 incoherent trials, each with 25 trials in CW and CCW directions. Trials were presented in a randomized order in blocks of 10 trials. Participants could take a self-timed break at the end of each block and between trials if necessary. Each session began with a short practice block (12 trials in a randomized order: 6 in each condition, with 3 in each direction) during which the participants could become familiar with the experimental procedure and self-calibrate their use of the vection strength scale. Following this practice, the EEG was prepared and the main experiment was conducted. No participant reported motion sickness and all participants completed the experiment.

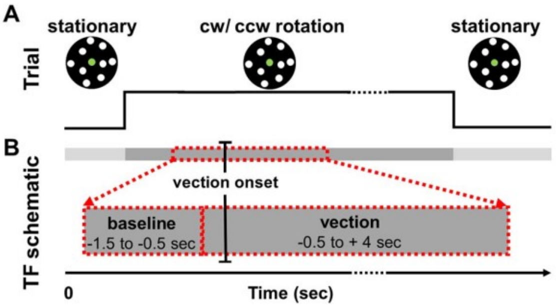

Fig. 1 **a** Trial schematic. Each trial began with stationary dots for a jittered period of between 3 and 5 s. The dots then began to rotate in a clockwise (CW) or counter-clockwise (CCW) direction for 20 s. During this time the participants reported vection onset/offset by means of a button push. The dots then became stationary for a period of 10 s. Participants verbally reported the strength of their vection experience after each trial. **b** Time–frequency (TF) schematic. The data for the TF analysis were extracted from the 20 s period of dot rotation in the coherent condition. The baseline window (− 1.5 to − 0.5 s) and the ongoing vection window (− 0.5 to + 4 s) were defined relative to reported vection onset (time 0)

EEG acquisition and preprocessing

The EEG was recorded using a 64 active electrode system (EASYCAP and BrainProducts, GmbH, Germany). The electrodes were placed according to the international 10–10 system with the reference electrode placed at FCz. Horizontal and vertical eye movements were recorded using bipolar electrode montages. The data were collected at a sampling rate of 1000 Hz, with no additional online filters. The active electrode impedances were kept below 5 kΩ throughout the recording. The EEG recording was synchronized with the visual motion stimulation and response controller using triggers sent via parallel port to the EEG recording. The EEG data were acquired using BrainVision Recorder software (BrainProducts, GmbH, Germany) and subsequently analysed using EEGLAB [35], custom scripts in MATLAB and FOOOF [36] in Python. The data preprocessing was performed in the following order. The data were re-referenced to the common average reference. Independent component analysis (ICA) was then used to decompose the data using the runICA function in EEGLAB. Components reflecting ocular noise, such as blinks or muscle artifacts were removed and the EEG signals were then reconstructed.

Fast Fourier transform (FFT) analysis

In order to compare the neural activity in the coherent and incoherent conditions, the data from motion onset to motion offset (i.e. 20 s of stimulus rotation data) was extracted for each participant. The CW and CCW trials were collapsed, resulting in 50 coherent and 50 incoherent trials per participant. Next, the 20 s of data in each trial was segmented in non-overlapping 1 s segments. In order to reduce the potential contribution of motor response artifacts or residual eye artifacts, any segment containing a button–push or channel signal exceeding 100 μV was rejected. The remaining segments were then multiplied with a Hanning window and spectra were computed using an FFT approach. A grand average was calculated for each participant, reflecting their respective spectral amplitude at each electrode position. Each participant's individual peak in the theta (4–7 Hz), alpha (7–14 Hz) and beta (20–30 Hz) bands were then identified using the FOOOF algorithm [36], with the peak being defined as the largest fitted peak, within the respective band, above the 1/f component of the spectrum. This resulted in an individual peak, i.e. in each frequency band, at each electrode in both the coherent and incoherent conditions for each participant.

Time–frequency (TF) analysis

In order to study the temporal dynamics of the alpha band activity at vection onset and during ongoing vection, a time–frequency (TF) decomposition was conducted on the coherent condition data. To be included in this analysis a trial had to (a) have at least 3 s between motion onset and vection onset and (b) have at least 5 s of continual ongoing vection after vection onset. For all trials meeting this criteria an 8 s window of data was extracted, ranging from 3 s before vection onset to 5 s after vection onset (i.e. − 3 s to + 5 s, with time 0 = vection onset). A Morlet wavelet transformation was used to calculate TF maps, linearly ranging from 3 to 40 Hz, for each participant across all segments. The wavelet had a width of 7 cycles. The TF maps were normalized for each participant with respect to a pre-vection interval (− 2.5 s to − 1.5 s relative to vection onset) using a decibel conversion. Next, regions of interest (ROIs) were defined separately for left and right handers based on the results of the FFT analysis. The left hander ROI consisted of electrodes CP1, P3, CP3, P1, P5, PO7 and PO3, while the right hander ROI consisted of electrodes Pz, CP2, P1, P2 and CPz. The spectral power in the alpha band was then averaged within the respective ROIs. The baseline window was defined as − 1.5 s to − 0.5 s (Fig. 1b) and the time points in this window were averaged, resulting in one value per participant. The vection window was defined as − 0.5 s to + 4 s (Fig. 1b), with each participant having one value per time point within this range.

Source localization

The exact low-resolution brain electromagnetic tomography algorithm (eLORETA), as developed and implemented by Pascual-Marqui [37, 38] and freely available through the LORETA webpage (https://www.uzh.ch/keyinst/loreta.htm), was used to estimate the location of EEG sources. The employed LORETA implementation uses a realistic head model [39] and restricts estimated solutions to cortical grey matter which is modelled by 6239 voxels of 5 mm resolution. The LORETA analysis included coherent condition trials in which vection was present and incoherent trials in which vection was absent. For coherent trials, each participant's mean time course within the vection window (i.e. − 0.5 to + 4 s relative to vection onset) was extracted and exported to LORETA. In the incoherent trials there was no vection onset and thus no clear window of data to extract. In this case, each participant's mean time course in a comparable window (i.e. 0.5 to + 4 s) was extracted and exported to LORETA, using their respective mean vection onset latency from the coherent condition as a marker (i.e. time = 0). A transformation matrix based on the coordinates of the electrode positions was created and applied to the coherent and incoherent data. To test for significant effects, paired samples *t* tests were conducted between the LORETA transformed coherent and incoherent conditions at each time point, for both left and right handers.

Statistics

Behavioural data

For both the coherent and incoherent conditions the following behavioural data were obtained for every trial: (1) vection presence, i.e. if vection was reported in a given trial, (2) onset latency, i.e. the time between motion onset and vection onset, (3) duration, i.e. how long the period of vection lasted and (4) vection strength, i.e. subjective rating of how strong the vection experience was from 0 = 'no vection' to 10 = 'I felt I was really moving'. To verify that CW and CCW trials could be appropriately collapsed, Wilcoxon signed-rank tests were conducted to compare each behavioural measure during CW versus CCW stimulation, within the coherent and incoherent conditions, for left and right handers, respectively. As no effect of stimulation direction was observed on any behavioural measure (Wilcoxon signed-rank tests, all $p > 0.05$, Bonferroni corrected), CW and CCW stimulus directions were collapsed within the coherent and incoherent conditions, for all subsequent analyses. Potential differences between left and right handers on behavioural measures were assessed using the non-parametric Wilcoxon rank sum test within both the coherent and incoherent conditions. Effect sizes were calculated as $r = Z/\sqrt{}$ (number of observations). An additional correlation analysis was conducted to investigate potential habituation of vection strength over the course of the experiment, for both the coherent and incoherent conditions. The vection strength scores for each subject were first normalized by subtracting their respective median score over all trials. The data were pooled for left and right handers and a Spearman's rank-order correlation was conducted to compare normalized vection strength over trials.

FFT analysis

Potential frequency band differences between the coherent and incoherent conditions were examined by means of nonparametric permutation testing, for left and right handers, respectively. The test examined whether there was a significant difference in power, at the individually defined peak, in the coherent versus incoherent conditions at each electrode, for each participant. Specifically, the peak values in the coherent and incoherent conditions were shuffled for each participant over 1000 iterations. Significance values were obtained by comparing the observed group test statistic with the null distribution by converting the observed test statistic into a standard *Z* value and then converting it to a

p value [40]. A cluster-based permutation test, following the procedure outlined in [41], was then implemented as a way to take the problem of multiple comparisons and data dependency into account in the statistical testing procedure. All electrodes for which the permuted Z value exceeded an a priori threshold ($p < 0.05$) were clustered on the basis of spatial adjacency. The data were then randomized over 1000 iterations to obtain a null distribution of the largest cluster Z values. This distribution was then compared against the observed cluster-level statistic (defined as the sum of the Z values within the cluster) and a p value calculated.

TF analysis

Potential differences in the alpha band activity around vection onset and during the course of ongoing vection were also assessed using nonparametric permutation testing, for left and right handers within their respective ROIs. In this instance the test examined whether there was a significant difference between the averaged baseline window (i.e. − 1.5 s to − 0.5 s relative to vection onset) and each time point in the vection window (i.e. − 0.5 s to + 4 s relative to vection onset). In detail, the alpha band value at baseline and in the vection window were shuffled for all time points, for each participant over 1000 iterations. Significance values were obtained as outlined above before a temporal cluster-based permutation test was conducted. In this instance, clusters were defined as having a minimum of 20 sequential time points for which the permuted Z value exceeded an a priori threshold ($p < 0.05$). The data were then randomized over 1000 iterations to obtain a null distribution of both the largest positive and negative cluster Z values. These distributions were then compared against their respective observed cluster-level statistic (defined as the sum of the Z values within the cluster) and p values calculated. All statistical analyses were conducted in MATLAB using custom scripts.

Results

Behavioural data

Vection presence

For each trial, the presence or absence of vection was recorded. These data were then summarized as the overall percentage of trials in which vection was reported as present for both the coherent and incoherent conditions. In the coherent condition, the median vection presence was 96% for left handers and 94% for right handers, with no significant difference ($Z = -0.66$, $p = 0.51$, $r = 0.13$). In the incoherent condition median vection presence reported was 4% for left handers and 8% for right handers, a difference which did not reach significance ($Z = -0.92$, $p = 0.36$, $r = -0.18$). Note that the vast difference in the percentage of trials in which vection was reported present between the coherent and incoherent conditions precludes meaningful statistical comparison between the two conditions.

Onset latency

In the coherent condition the median onset latency was 5.96 s for left handers and 5.61 s for right handers, with no significant difference ($Z = -0.27$, $p = 0.79$, $r = -$ -0.05). In the incoherent condition, the left handers had a median onset latency of 10.72 s, with the right handers having a median of 12.66 s, a difference which did not reach significance ($Z = -1.12$, $p = 0.26$, $r = -0.22$).

Duration

In the coherent condition, a median vection duration of 12.48 s and 13.16 s was reported for left and right handers, respectively, with no significant difference between the groups ($Z = 0.11$, $p = 0.91$, $r = 0.02$). In the coherent condition the left handers had a median duration of 5.07 s, with the right handers having a median duration of 3.86 s, a difference which did not reach statistical significance ($Z = 0.37$, $p = 0.71$, $r = 0.07$).

Vection strength

The median vection strength reported in the coherent condition was 5.00 for left handers and 5.50 for right handers, with no significant statistical difference between the two groups ($Z = -1.25$, $p = 0.21$, $r = -0.25$). In the incoherent condition the median vection strength was 0 for both left and right handers, with no significant difference between the two groups ($Z = -0.06$, $p = 0.96$, $r = -0.01$). The Spearman's rank-order correlation revealed a small negative correlation, with vection strength decreasing over trials for both the coherent ($r_s = -0.08$, $p < 0.001$) and incoherent conditions ($r_s = -0.08$, $p < 0.001$). This small negative correlation corresponds to a mean decrease of vection strength by 0.24 in the coherent condition and 0.35 in the incoherent condition, between the start and end of the experiment (mean of first 10 versus last 10 trials).

In summary, in both the coherent and incoherent conditions no statistically significant differences were observed between left and right handers on measures of vection presence, onset latency, duration and vection strength (Fig. 2).

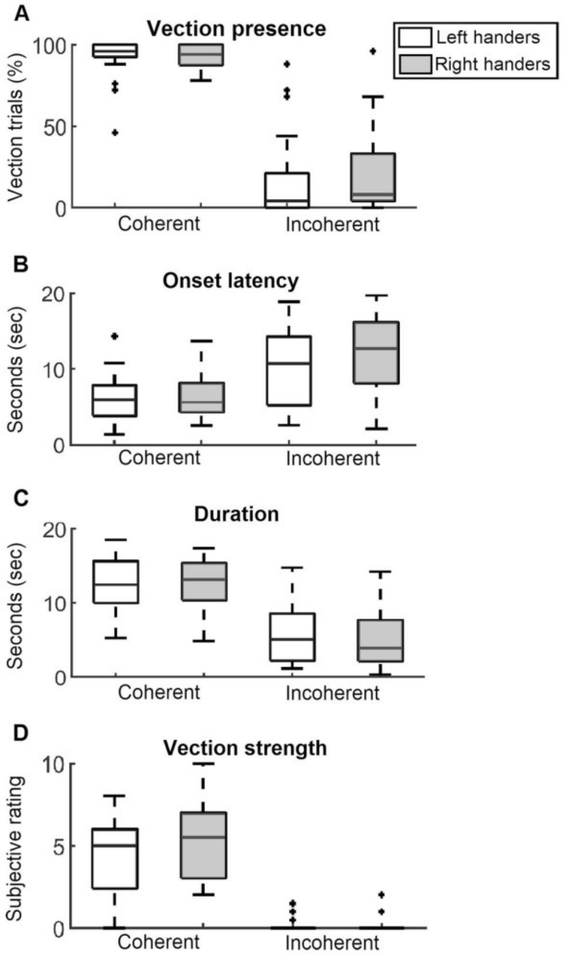

Fig. 2 Behavioural data. **a** Vection presence, i.e. percentage of trials in which vection was reported as present. **b** Onset latency, i.e. time from motion onset to vection onset, in seconds. **c** Duration, i.e. length of vection period, in seconds. **d** Vection strength ratings on a scale of 0 ('no vection') to 10 ('I felt I was really moving'). Each panel presents a boxplot with the median group value for the coherent and incoherent conditions, for both left (white) and right (grey) handers. The box around the median represents the 25th and 75th percentile, with the whiskers extending to the most extreme scores. Crosses represent outliers, calculated as values greater than $q3 + w \times (q3 - q1)$ or less than $q1 - w \times (q3 - q1)$, where w is the maximum whisker length and $q1$ and $q3$ are the 25th and 75th percentiles, respectively

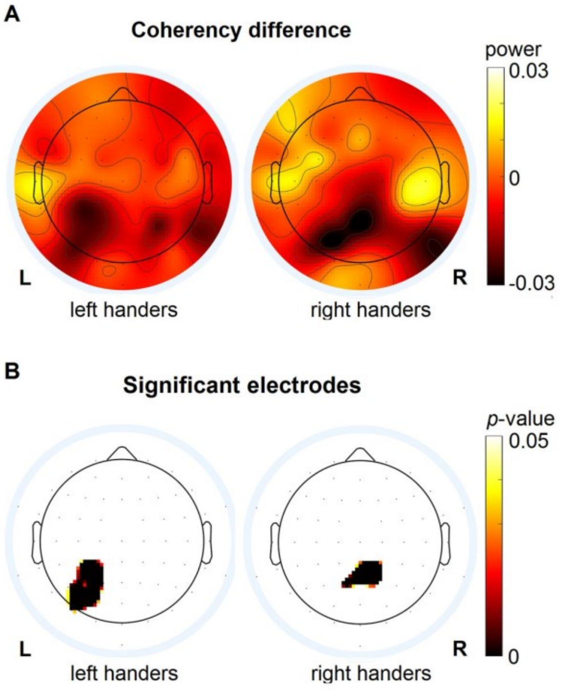

Fig. 3 Coherent versus incoherent visual stimulation (FFT analysis). **a** Coherency difference: Topographies showing group–level coherency difference, i.e. coherent condition minus incoherent condition, in alpha power for left and right handers, respectively. **b** Significant electrodes: Topographies showing the largest cluster of electrodes in which alpha power differed significantly between the coherent and incoherent conditions, i.e. $p < 0.05$ after cluster-based permutation testing, for both left and right handers. Both groups showed a decrease in alpha power in the coherent relative to incoherent condition. For left handers (bottom left) the significant reduction in alpha power in the coherent condition was visible at a left centro-parietal region including electrodes CP1, P3, CP3, P1, P5, PO7, and PO3, while right handers (bottom right) showed the effect at a midline centro-parietal region including electrodes Pz, CP2, P1, P2 and CPz

EEG data

Coherent versus incoherent visual stimulation (FFT analysis)

Potential differences in theta, alpha and beta activity between the coherent and incoherent conditions were examined by statistically comparing the obtained power between both conditions, at each electrode, for left and right handers, respectively. Significant differences between the coherent and incoherent conditions were observed only in the alpha band.

The mean difference in alpha power between the coherent and incoherent conditions, i.e. coherent minus incoherent, for both left and right handers, is illustrated in Fig. 3a. After cluster-based permutation testing to deal with the issue of multiple comparisons, significant differences between the coherent and incoherent conditions were observed for both left and right handers (Fig. 3b). For left handers, there was a significant difference between coherent and incoherent conditions at a left centro-parietal cluster, including electrodes CP1 P3, CP3, P1, P5, PO7 and PO3 ($p = 0.0004$). Right handers showed a significant difference between the coherent and incoherent conditions at a midline centro-parietal cluster, including electrodes Pz, CP2, P1, P2 and CPz ($p = 0.02$). In both instances, the statistical differences were driven by a *decrease* in alpha power in the coherent condition relative to the incoherent condition. Notably, the behavioural data (Fig. 2) descriptively show that the experience of vection was more intense in the coherent than incoherent condition, i.e. present on more trials, shorter onset latency, longer duration and stronger subjective experience. Indeed, on a group level vection was reported as occurring on as little as 4% and 8% of trials for left and right handers, respectively, in the incoherent condition, meaning this condition was less vection compatible than the coherent condition. Combined with the present results, this would indicate that alpha power decreased during a vection compatible stimulus, i.e. coherent condition, relative to a comparable stimulus which was less likely to induce vection, i.e. incoherent condition. In other words, the decrease in alpha power appears to occur in the presence of vection, with the effect being observed at distinct electrode clusters for both left and right handers.

Temporal dynamics of vection (TF analysis)

The temporal dynamics of alpha band activity during the course of vection were examined by statistically comparing the alpha power observed in the averaged baseline window, i.e. – 1.5 s to – 0.5 s relative to vection onset, with the alpha power observed at each time point in the vection window, i.e. – 0.5 s to + 4 s relative to vection onset (Fig. 4). This analysis was conducted on coherent trials only, with separate ROIs being used for left and right handers, i.e. ROIs were defined as the clusters of electrodes which differed significantly between the coherent and incoherent conditions. For left handers, cluster-based permutation testing revealed two periods of time in which alpha power differed significantly between the baseline and vection windows. Firstly, relative to baseline there was a significant *decrease* in alpha band power prior to vection onset ($p < 0.001$, from – 0.47 to – 0.34 s relative to vection onset). Secondly, relative to baseline there was a significant *increase* in alpha power during ongoing vection ($p < 0.001$, from + 1.63 to + 3.98 s relative to vection onset). For right handers a significant increase in alpha power, relative to baseline, was observed during ongoing vection ($p < 0.001$, from + 3.02 to + 3.98 s relative to vection onset). Notably, both groups demonstrated earlier significant increases in alpha band power during ongoing vection (left handers: from + 1.13 to + 1.62 s; right handers: from + 2.36 to + 2.73 s). However, as the cluster-based permutation testing was conducted on the maximal positive and negative clusters, these remain uncorrected for multiple comparisons. In summary, these results show that alpha power decreased prior to vection onset (significant for left handers only) and increased during ongoing vection.

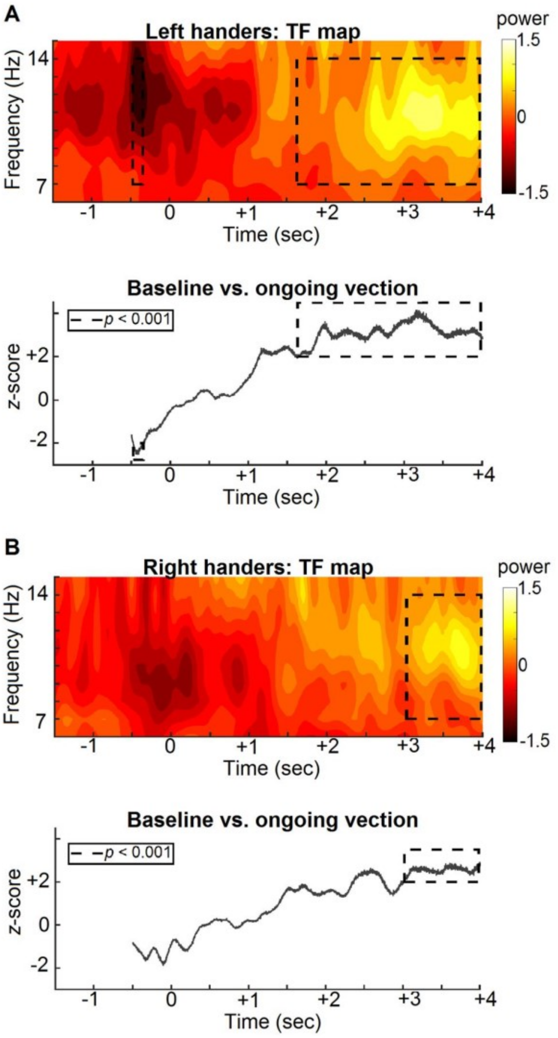

Fig. 4 Temporal dynamics of vection (TF analysis) at handedness-specific ROIs for left handers (**a**) and right handers (**b**). *Time frequency (TF) maps* show changes in alpha power time locked to vection onset, i.e. time 0. *Baseline vs. ongoing vection maps* show the z score difference in alpha power between the baseline window, i.e. – 1.5 s to – 0.5 s, and the ongoing vection window, i.e. – 0.5 s to + 4 s, at each time point. Regions surrounded by black dotted lines are significant at $p < 0.001$ after cluster-based permutation testing. Both left and right handers show similar changes in alpha power over the course of vection, with a decrease in power being observed around the time of vection onset (significant for left handers only) and an increase in power being observed during ongoing vection

Source localization

For both left and right handers, comparison of the LORETA transformed coherent and incoherent conditions returned non-significant results ($p > 0.05$). Although non-significant, the maximal differences between coherent and incoherent conditions included a number of regions associated with the vestibular network [21, 28]. For left handers, the maximum differences were observed at left postcentral gyrus, precentral gyrus and inferior parietal lobule. For right handers, the maximal differences were observed at left inferior parietal lobule, postcentral gyrus, inferior frontal gyrus, precuneus, insula and right paracentral lobule.

Discussion

The present study examined the behavioural characteristics and neural correlates of visually induced vection in left and right handed participants. Our results found no difference between left and right handers on behavioural measures of vection, i.e. presence, onset, duration and subjective strength, in either the coherent vection–compatible condition or the incoherent control condition. Additionally, we found no evidence amongst left and right handers to suggest that these behavioural measures of vection are modulated by stimulus direction (i.e. CW versus CCW). The results of the FFT analysis demonstrated a significant decrease in alpha power in the coherent relative to incoherent conditions, for both left and right handers. Notably, this difference was observed in different topographical regions, with left handers demonstrating a decrease in left centro-parietal electrodes and right handers showing a decrease at midline centro-parietal electrodes (Fig. 3). Neither left nor right handers exhibited significant differences in theta or beta band activity between the two conditions. In order to further investigate the relationship between alpha power and vection, a time–frequency analysis, time locked to vection onset was conducted. The results of this analysis found significant changes in alpha power during the course of vection, with similar patterns being observed for left and right handers. The present study is the first comparison of the behavioural characteristics and neural patterns of roll vection across left and right handers. The implications of our study findings for our understanding of visual self-motion are discussed below.

Behavioural characteristics of roll vection are independent of handedness

In the present study, left and right handers demonstrated remarkably similar vection characteristics with almost identical scores on measures of vection presence, onset latency, duration and subjective strength, for both coherent and incoherent conditions. To some extent this finding contradicts the recent observation that right handers display quicker perceptual transitions from world- to self-motion (i.e. vection onset latency), compared to left handers [42]. One possible explanation for the discrepancy between these findings is differences in the employed visual motion stimuli and the vection they induced. In the previous study, the optokinetic stimuli consisted of a drum marked with vertical black and white lines, which rotated around the participant in the earth-vertical axis, inducing circular vection. In contrast, the visual motion stimuli used in the present study consisted of white dots on a black background, rotating along the roll axis, inducing the perception of roll vection. Notably, the onset latencies in the present study were considerably shorter than those reported in the previous study [42], which could be indicative of a more intense vection experience resulting in less subjective variation on behavioural measures across participants. Although literature on the topic is sparse, there is some evidence showing differences in onset latency [1] and subjective intensity [4] across different types of vection, i.e. along different planes/axes. Indeed, different types of motion stimuli have also been found to show different patterns of neural activation both in the absence [43] and presence [4] of vection. Such findings make it difficult to compare and interpret the relevance of differences in onset latency findings between this and the previous study. A small negative correlation, across both left and right handers, revealed that vection strength decreased very slightly over the course of the experiment. Crucially, this small decrease in perceived vection strength was comparable across the coherent and incoherent conditions, suggesting that both conditions were comparably affected by slight vection habituation over time. In summary, the behavioural data indicate that left and right handers experience roll vection in a similar manner.

Alpha power is decreased during vection induced by visual motion stimulation

In our study, both left and right handers exhibited decreases in alpha power whilst viewing a vection–compatible visual motion stimulus, in contrast to a control stimulus. Determining whether changes in activation patterns reflect visual motion stimulation in general, differences between experimental and control conditions and/or vection itself is experimentally challenging. For example, studies which contrast vection-inducing visual motion stimuli with static control stimuli, e.g. [4, 44], likely include activation changes that reflect the difference between stationary and moving stimuli, irrespective of whether or not vection was present. Also, contrasts between coherent and incoherent/random motion stimuli may result in activation changes which are attributable to physical stimulus differences rather than vection per se [2, 45]. As such, it is apt to examine the extent to which the decrease in alpha power, observed in the present study, can be attributed to vection.

Firstly, the behavioural results clearly demonstrate that on the group level, vection was almost always present in the coherent visual motion condition (i.e. on 96% and 94% of trials for left and right handers, respectively) but rarely, if ever, present in the incoherent visual motion condition (i.e. on 4% and 8% of trials for left and right handers, respectively). This demonstrates that the observed decrease in alpha power is associated with the presence of vection. Secondly, the incoherent visual control stimulus was designed such its physical stimulus properties matched those of the coherent stimulus as closely as possible. Although the incoherent stimulus contained additional local sinusoidal motion, both stimuli presented the same average global velocity. Physical stimulus differences would have likely produced differences in occipital activations between the two conditions, reflecting early visual processing. The absence of such occipital activations in our results suggests that our findings are not attributable to differences between the employed stimuli. Furthermore, this also indicates that the observed differences contain limited, if any, activity related to the processing of visual motion stimulation rather than vection per se. Lastly, subsequent time–frequency analysis of vection-present coherent trials, showed changes in alpha power which were time locked to vection onset, for both left and right handers. This provides further evidence that the changes in alpha power observed in this study are related to vection, rather than general visual motion stimulation.

Left and right handers show differences and similarities in vection related alpha power changes

A key finding in this study is that the decrease in alpha power that results from exposure to a vection compatible stimulus is observed at different topographical regions for left and right handers. Left handers exhibited a lateralized response to the vection stimulus over a left centro-parietal region. In contrast, right handers showed a bilateral response in a midline centro-parietal area (Fig. 3). Multiple comparisons can be drawn between these findings and the existing literature. First, although non-significant, the source localization results suggest that the vection-compatible stimulus, which results in different activity patterns for left and right handers, and the incoherent stimulus are maximally different at regions within the vestibular network. Although further research is required to substantiate this finding, it is congruent with the established idea that visually-induced vection relies on visual–vestibular interaction [2]. Secondly, in contrast to previous fMRI and PET studies [2–5], which demonstrate vection-related activation of visual cortex and concurrent deactivation of PIVC, the present study found that vection is associated with activity changes at centro-parietal regions. This discrepancy could be explained by a number of factors including our use of a novel control stimulus which controlled for low-level visual properties and average global motion, and also to differences in the type of activity and spatial resolution measured by EEG, fMRI and PET. Lastly, the observation that left and right handers show vection-related alpha band changes at different topographical regions is congruent with fMRI and PET studies demonstrating handedness-dependent vestibular thalamo-cortical dominance [17–28]. Notably, while such studies show vestibular dominance in the right hemisphere in right handers and in the left hemisphere for left handers, the present study found a bilateral activation for right handers and a left-lateralized activation for left handers.

Given the topographical differences in vection-related activity for left and right handers, subsequent time–frequency analyses were conducted separately for both groups in order to maximize our ability to examine the neural correlates of vection within each group. Despite the topographical differences in where vection-related activity was observed, both left and right handers exhibited a similar pattern of alpha band changes over the course of vection. Both groups showed decreased alpha power around vection onset (significant only for left handers) and increased alpha power during ongoing vection (Fig. 4). These findings not only compliment those of a recent EEG study examining the neural correlates of vection in right-handed participants [31], but also extend the findings to left handers. Notably, left handers appear to show increased alpha power during vection much earlier than right handers in our study. However, as both groups demonstrate the same trend of increasing alpha power during ongoing vection and that the measures of alpha power come from different topographical regions, we are hesitant to label this temporal discrepancy as an effect of handedness. The observation that left and right handers show similar alpha patterns during the course of vection matches well with our observation of comparable behavioural characteristics between the two groups and suggests that vection and its respective processes are consistent across handedness, despite those same processes being observed at different topographical regions in a handedness-dependent manner.

A role for alpha oscillations in visually-induced vection

This study made two key observations about alpha oscillations in relation to vection: (1) a decrease in alpha power is observed during exposure to a vection-compatible stimulus, relative to a matched control and (2) both decreases and increases in alpha power are observed during the course of vection. Beginning with the former, the decrease in alpha power during exposure to a vection compatible stimulus is consistent with desynchronization and a release from inhibition [46], correlating with excited neural structures or activated cortical areas [47]. This would suggest that exposure to a vection compatible stimulus induces increased activity in centro-parietal regions, with the effect being (midline) bilateral for right handers and left-lateralized for left handers. Evidence exploring the relationship between alpha oscillations and activations observed in fMRI and PET imaging suggests that alpha power is negatively correlated with the blood-oxygen-level-dependent (BOLD) signal [48] and also with regional cerebral blood flow (rCBF) in primary and association visual cortex [49]. Although the origins of the alpha oscillations observed in this study are unclear, the inverse relationship between alpha power and cortical activation suggests that the observed decrease in alpha power in the present study maps well with findings of increased activation of parieto-occipital regions in previous vection studies [2, 4]. Such previous studies employed only right handed participants and therefore, it is unclear whether spatial differences between left and right handers similar to those observed in this study, would also present themselves in parieto-occipital activations in PET and fMRI studies.

Although our findings indicate a clear link between alpha oscillations and vection, the exact nature of this relationship requires further investigation. The first possibility is that the decrease in alpha power reflects an increase in cortical activation which is compatible with an inhibitory visual–vestibular interaction. This increased activation could operate by amplifying visual signals over vestibular signals such that the visual dominates or by triggering inhibition of vestibular cortex itself. A second possibility is that decreased alpha power reflects an inhibitory visual–visual interaction, with the increased activation either amplifying visual signals consistent with self-motion over those consistent with object–motion or even triggering inhibition of visual object–motion processing.

A third possibility is that the decreased alpha and increased activation reflect additional attentional processes involved in vection perception. It is possible that the sensation of self-motion and/or the sensory mismatch involved in vection perception might require or induce additional attentional processes which involve increased cortical activation. For example, alpha desynchronization has also been observed during turning movements in virtual reality environments, with stronger decreases occurring when there is incongruency between sensory modalities and thus, increased demands on visuospatial attention [50]. Furthermore, the observed decrease in alpha power in the present study could also reflect top-down attentional control. Vection requires that visual motion is interpreted as resulting from self-motion rather than environmental motion. This erroneous interpretation can be explained by our a priori anticipation that the external world is stable, making it more probable that motion cues are attributable to self-motion [1]. In terms of visual processing, anticipatory alpha band modulations have been implicated in the top-down allocation of selective visuospatial attention [51]. Further, the amplitude of alpha desynchronization has been shown to follow the time course of temporal expectation, suggesting that alpha oscillations have a role in the regulation of cortical excitability as a function of anticipatory visuospatial attention and may act as a mechanism for biasing perception [52]. Indeed, in addition to the decreases in alpha power during exposure to a vection compatible stimulus, the time–frequency analyses also revealed a decrease in alpha power beginning prior to vection onset. In this context, this finding could be interpreted to reflect top-down attentional control and anticipation of vection. This decrease in alpha power around the time of vection onset is also consistent with the literature on bistable perception, in which decreasing alpha power is thought to reflect destabilization of the current percept, with decreases beyond a given threshold resulting in the development of the alternative percept [32, 34].

During ongoing vection, we observed an increase in alpha power, which has been shown to be associated with increased inhibition and reduced activation [46]. On one hand, this increase in alpha power during ongoing vection could be a result of object–motion compatible signals and/or vestibular signals (i.e. indicating a lack of self-motion) exerting a reciprocal inhibition on visual self-motion signals. The temporal characteristics of vection vary widely between participants and in order to ensure sufficient trials for analysis and that there was no contamination from changes in alpha power due to vection or stimulus offset, we selected a very limited time window for our analysis of ongoing vection. Unfortunately, this means that we do not know if alpha power continued to increase beyond our window of investigation and if that decrease would ultimately lead to the breakdown of vection. An alternative explanation for the increased alpha power is that while an initial decrease in alpha and an associated increase in activity, is necessary for one perceptual interpretation (i.e. self-motion) to become dominant, the dominant percept can be sustained without continuing increased activation, thus allowing a shift to a less active baseline state with greater alpha power. We propose that future studies combining EEG and non-invasive brain stimulation techniques (e.g. TMS) or positron emission tomography (PET) are necessary to disentangle the role of alpha power increases and decreases and to establish a causal link between alpha oscillations and vection.

Conclusion

This study examined the behavioural characteristics and neural correlates of roll vection in left and right handers. We found that vection-related alpha power changes occur at different topographical regions for left and right handers. Despite these spatial differences, both left and right handers exhibit similar behavioural characteristics and patterns of alpha band changes during ongoing vection.

Availability of data/materials

Data are not publicly available due to the constraints of the ethical approval for the study. Example code is available from the corresponding author on reasonable request.

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Author contributions MM, TB and MD contributed to the study conception and design. Data collection was performed by MM. Data analysis was conducted by MM, JD and VK. All authors contributed to and approved the final manuscript.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval The study was conducted in accordance with the institutional ethics committee standards and the Declaration of Helsinki.

Informed consent Informed written consent was obtained from participants prior to their involvement in the study. Participants were informed of their right to withdraw from the study at any point.

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2.2 Study 2: EEG analysis of the visual motion activated vection network in left- and right-handers

The manuscript resulting from this project has been submitted for publication at a peer-reviewed journal (Scientific Reports).

Author contributions:

Michaela McAssey, Marianne Dieterich, and Thomas Brandt conceived the experiment. Michaela McAssey collected the data. Michaela McAssey analysed the data. Michaela McAssey drafted the manuscript, with feedback and revisions from Marianne Dieterich and Thomas Brandt. All authors commented on and approved the final manuscript. Michaela McAssey is the only first author of the paper.

EEG analysis of the visual motion activated vection network in left- and right-handers

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Abstract

Visually-induced self-motion perception (vection) relies on interaction of the visual and vestibular systems. Neuroimaging studies have identified a lateralization of the thalamo-cortical multisensory vestibular network, with left-handers exhibiting a dominance of the left hemisphere and right-handers exhibiting a dominance of the right hemisphere. Using electroencephalography (EEG), we compare the early processing of a vection-compatible visual motion stimulus against a vection-incompatible stimulus, to investigate the temporal activation of the vection network by visual motion stimulation and the lateralization of these processes in left- versus right-handers. In both groups, vection-compatible stimulation evoked attenuated central event-related potentials (ERPs) in an early (160 – 220 ms) and a late (260 - 300 ms) time window. Differences in estimated source activity were found across visual, sensorimotor, and multisensory vestibular cortex in the early window, and were observed primarily in the posterior cingulate, retrosplenial cortex, and precuneus in the late window. Group comparisons revealed a larger ERP condition difference (i.e., vection-compatible stimulation minus vection-incompatible stimulation) in left-handers, which was accompanied by group differences in the cingulate sulcus visual (CSv) area. Together, these results suggest that handedness may influence ERP responses and activity in area CSv during vection-compatible and vection-incompatible visual motion stimulation.

Keywords

Roll vection, self-motion perception, handedness, visual-vestibular interaction, EEG analysis, event-related potential (ERP), eLORETA

Introduction

Perception of self-motion relies on the integration of information from multiple modalities including the visual, vestibular, somatosensory, and auditory sensory systems. Although each system relays information relevant for determining self-motion perception, the visual system exerts a dominant influence. This is demonstrated by the fact that a physically stationary observer experiences an erroneous sensation of apparent self-motion, called visually induced vection, when exposed to large-field visual motion stimulation[1]. Vection typically takes several seconds to develop following motion onset and perception tends to fluctuate between periods of vection and object-motion perception during prolonged motion exposure[1]. Further, the characteristics of vection perception are largely subjective, with the same visual motion stimulus often generating highly variable onset latencies and strength/intensity reports both between and within individuals[2,3].

Several positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies have identified a large cortical network involved in vection perception. Early imaging studies reported an activation of primary and secondary visual cortices along with concurrent deactivation of multisensory vestibular cortex - primarily in the parieto-insular vestibular cortex (PIVC) - during exposure to vection-inducing motion stimulation[4–6]. This activation-deactivation pattern is thought to reflect an inhibitory visual-vestibular interaction mechanism for self-motion perception, which enables the dominant sensorial weight to shift from one sensory modality to another, presently more reliable modality[4,7]. While this activation-deactivation pattern is associated with vection perception, it is not solely responsible for, nor indicative of vection. Indeed, several studies have observed similar activation-deactivation patterns in visual and vestibular networks, regardless of vection presence[8–10]. Such observations indicate that the PIVC likely responds to motion stimulation in general, with deactivations encoding an absence of primary vestibular input during vection-compatible visual motion stimulation[9,11]. This information from the PIVC feeds into the wider multisensory cortical vestibular network, contributing to the visual-vestibular interaction underlying vection.

In line with the hypothesis that vection perception involves visual-vestibular interaction, vection-specific activity has been located in the superior parietal lobule/precuneus, the anterior cingulate gyrus, the right post-central region and the cerebellar vermis[9]. Further, a recent review of the literature identified a probable cortical vection network, including visual area V3, motion area V6, area MT+ and the superior middle temporal area (MST), the ventral intra-parietal area (VIP), the parieto-insular vestibular cortex (PIVC), and the visual area of the cingulate sulcus (CSv)[12]. This cortical vection network overlaps substantially with a proposed network for cortical optic flow parsing[13]. This latter network identifies the CSv area, cingulate motor area (CMA), parieto-insular cortex (PIC), and lateral occipital region (LOR) as regions that not only prefer self-motion information, but also respond negatively to object-motion information. Further, this network identifies an important role of the precuneus and cingulate region in the processing of ego-motion information[13].

While early PET/fMRI studies of vection have contributed much to our understanding of vection, the resulting findings are constrained by several methodological limitations. For example, the relatively low temporal resolution offered by these methods may fail to capture core aspects of vection, such as the brain processes involved in the relatively rapid alternations between object- and self-motion perception. Further, such studies often require participants to lie supine, which itself alters the visual-vestibular conflict with respect to the gravity vector (e.g., a sensory mismatch between visually induced continuous apparent self-rotation in yaw and a limited body tilt by graviceptive otolith input about true verticality). Lastly, the use of MRI itself may activate the vestibular system[14,15], thus extra care must be taken to ensure that effects observed in the multisensory cortical vestibular network can be attributed to vection specifically.

Electroencephalography (EEG) not only circumvents these methodological limitations but may also prove useful for identifying objective neural markers of vection[16,17]. For example, initial EEG studies have identified a role of alpha-band oscillatory activity in vection perception[18–21], with some evidence to suggest that alpha activity decreases around the time of vection onset[20,21]. Further, studies investigating early event-related potential (ERP) responses to visual motion stimuli that subsequently induce vection under prolonged exposure have indicated a potential relationship between N2 component amplitude and the subjective experience of vection[22–24].

While traditional neuroimaging and EEG approaches have both yielded insight into the neural mechanisms of vection perception, attempts to reconcile and integrate findings from both approaches are lacking. One potential explanation for this is that localising the source of EEG activity obtained at the scalp is a challenging and ill-posed problem. However, several algorithms to estimate the location of EEG sources now exist. One such algorithm is the low-resolution brain electromagnetic tomography algorithm (LORETA), whose accuracy has been demonstrated by EEG-PET[25] and EEG-fMRI[26] studies, including spatially complex regions like the insula[27], which forms a core part of the multisensory cortical vestibular network.

The present study combines ERPs and source localization (eLORETA) to investigate the early neural processing of a coherent motion stimulus that induces vection under prolonged exposure, against that of a vection-incompatible control stimulus. While our recent work indicated comparable vection perception in left- and right-handed individuals[21], a lateralization of the thalamo-cortical multisensory vestibular network is well established, with left-handers exhibiting a left-hemisphere dominance and right-handers exhibiting a right-hemisphere dominance[28–34]. Thus, the present study has two major aims: 1) to disclose the temporal activation of the vection network by visual motion stimulation, and 2) to examine the hemispheric lateralization of these processes in left- versus right-handers.

Methods

Participants

Thirty-five right-handed (17 female, mean age: 27.69 years, SD: 3.94) and thirty left-handed (22 female, mean age: 25.27 years, SD: 3.96) healthy adults participated in the study. All participants reported normal or corrected-to-normal vision and no prior history of vestibular or neurological disorders. The 10-item Edinburgh Handedness Inventory[35] was used to determine handedness for each participant (right handers: 5.7% ≥ +40, 11.4% ≥ +60, 8.6% ≥ +70, 17.1% ≥ +80, 57.1% ≥+90; left handers: 6.6% ≥ -40, 3.3% ≥ -50, 23.3% ≥ -60, 23.3% ≥ -70, 20% ≥ -80, 23.3% ≥ -90). Experimental protocols were approved by the local ethics committee at the Ludwig-Maximilians-University, Munich, Germany and all methods were carried out in accordance with relevant guidelines and regulations. All participants gave their informed written consent prior to their participation and received either financial compensation (€10/hour) or partial course credit.

Following initial preprocessing, 6 right-handed and 2 left-handed participants were excluded from the EEG analyses due to poor data quality (i.e., fewer than 30 artefact-free trials per condition). This resulted in a final EEG sample size of 29 right-handed and 28 left-handed participants. No participants were excluded from the behavioural analyses. Part of the data from the first 25 right-handers and 25 left-handers was included in separate analyses as part of a different study[21].

Visual motion stimulation

The visual motion stimulation used in the present experiment is identical to that reported in our previous study[21]. In brief, the stimuli comprised two movies: a coherent and an incoherent pattern of rotating dots. Both stimuli consisted of 1000 randomly spaced white dots on a black background, with a central green dot as the fixation point. The dots rotated in the roll plane in either a clockwise (CW) or counter-clockwise (CCW) direction, at a velocity of 30°/s. In the coherent condition, the rotation of the dots followed a smooth, circular trajectory. In the incoherent condition, a random sinusoidal movement was added to each dot, such that every dot appeared to move in a random path, despite the global pattern maintaining a (CW or CCW) circular trajectory and a mean global velocity of 30°/s. The stimuli were created in MATLAB (The MathWorks Inc., Natick, MA, USA) using Psychophysics Toolbox extensions[36–38] and were presented using a custom-built dome (diameter: 75 cm). The stimuli rotated around the line of sight and covered the entire field of view.

Experimental procedure

For each participant the experimental apparatus was adjusted to ensure that the dome-centre and line of sight were aligned. On each trial, the presented dots first appeared stationary for a jittered period (3-5 sec), before rotating (20 sec) and then returning to stationary (10 sec). Participants reported perceived vection onset and offset by making button presses on a gaming controller. Separate buttons denoted perceived CW and perceived CCW vection onset/offset. Participants held the controller in both hands and used both middle and index fingers to make responses. At the end of each trial participants were asked to verbally rate the strength of their vection experience on a scale of 0 to 10, where 0 is ‘no vection’ and 10 is ‘I felt I was really moving’. The response was recorded by the experimenter. Participants were seated with their head on a chin rest and were instructed to maintain fixation on the central green dot for the duration of each trial. Participants were also instructed to avoid following the moving dots with their eyes. Each participant completed 100 trials: 50 coherent trials and 50 incoherent trials, each with 25 trials in CW and CCW directions. Trial order was random, with trials presented in blocks of 10. Participants were encouraged to take a self-timed break at the end of each block, and between trials if necessary, in order to prevent fatigue.

Prior to the main experiment, each participant completed a short practice block comprising 12 trials presented in a random order (6 trials per condition, with 3 in each direction). The practice allowed participants to become familiar with the experimental task and to self-calibrate their use of the vection strength scale.

EEG acquisition

The EEG was recorded using a 64 active electrode system (EASYCAP and BrainProducts, GmbH, Germany) with BrainVision Recorder software (BrainProducts, GmbH, Germany). Electrodes were fixed to standardized elastic caps following the international 10-10 system. The reference electrode was positioned at FCz. Bipolar electrode montages were used to record horizontal and vertical eye movements (i.e., EOG). Data were collected at a sampling rate of 1000 Hz, with no additional online filters. Impedances were kept below 5 kΩ throughout the recording. The EEG, visual motion stimulation, and response controller were synchronized using triggers sent via parallel port to the EEG recording. This enabled the accurate calculation of vection onset latency and duration based on participant button presses, and the computation of ERPs that were time-locked to stimulus motion onset.

EEG preprocessing and ERP computation

Preprocessing and analysis were performed using the EEGLAB toolbox[39] and custom MATLAB scripts. A 50 Hz and 100 Hz notch filter was applied to remove line noise using the CleanLine plugin[40]. A 0.1 Hz high-pass filter and a 30 Hz low-pass filter were then applied before re-referencing the data to the common average. The data were segmented into 600 ms epochs, ranging from -200 ms to +400 ms, relative to stimulus motion onset. The 200 ms pre-stimulus interval served as the baseline period for baseline correction. Epochs containing eye blinks, eye movements, or excessive signal range were excluded from analysis. To identify epochs for rejection, each epoch was segmented into a 200 ms window using a sliding window moving at 50 ms intervals. An epoch was rejected if any given 200 ms window was found to contain a) a standard deviation greater than 35 µV in the EOG, Fp1, Fp2, or Fz electrodes or b) if the signal range exceeded 100 µV. To ensure a sufficiently high signal-to-noise ratio of the ERP averages, trials in the CW and CCW directions were collapsed within the coherent and incoherent conditions. Participants were excluded from EEG analyses if fewer than 30 artefact-free epochs (i.e., trials), in two or more electrodes, were obtained for either the coherent or the incoherent condition. This resulted in the exclusion of 6 right-handed and 2 left-handed participants from the EEG analyses.

Grand average ERPs, time-locked to stimulus motion onset, were computed separately for the coherent and incoherent conditions, for left- and right-handers respectively. Condition difference waves (i.e., coherent minus incoherent) were also computed separately for both groups. Following visual inspection, two time windows were identified for further analysis: an early window ranging from 160 – 220 ms and a later window ranging from 260 – 300 ms. Mean amplitude within these time windows was calculated at each electrode, for coherent and incoherent conditions, as well as for difference waves, for both left- and right-handers.

Source localization (eLORETA)

The exact low-resolution brain electromagnetic tomography algorithm (eLORETA) developed and implemented by Pascual-Marqui[41,42], and freely available from the LORETA webpage (http://www.uzh.ch/keyinst/loreta.htm), was used to estimate the most likely generators of the observed ERP signals. For both conditions, the average ERP time series of each participant were exported to LORETA and a transformation matrix was applied. The first analysis aimed to identify generator differences between the coherent and incoherent conditions, for left- and right-handers respectively. To this end, the mean activity in the early and late windows was compared between conditions, separately for left- and right-handers. Significant effects were tested using paired-group t-statistic contrasts (5000 randomisations SnPM, significance threshold of $p < 0.05$). A second analysis aimed to identify generators that might explain differences between left- and right-hander condition difference waves. An independent groups test was conducted, (t-statistic, 5000 randomisations SnPM, significance threshold of $p < 0.05$), comparing the coherent minus incoherent localised activity of right-handers to that of left-handers. Again, tests were conducted for the mean over early and late windows. Suprathreshold voxels in each analysis were labelled in MATLAB using the mni2atlas tool[43] and the Juelich histological and Harvard-Oxford atlases as implemented in FSL[44]. Our results were compared against those in previous studies for area CSv[45] and the retrosplenial cortex[46,47].

Statistical analyses

Statistical analyses were conducted in MATLAB. Figures were created using custom MATLAB scripts, with the cbrewer tool[48], and MRIcroGL[49].

Behavioural data. The following behavioural data were obtained on each trial: (1) vection presence, i.e., if vection was reported, (2) onset latency, i.e., the time between motion onset and vection onset, (3) duration, i.e., how long a period of vection lasted, and (4) vection strength, i.e., subjective rating of how strong the vection experience was. In-line with the EEG analyses, CW and CCW trials were collapsed within coherent and incoherent conditions. For each behavioural measure, potential differences between left- and right-handers were assessed using the non-parametric Wilcoxon rank sum test. Separate tests were conducted for coherent and incoherent conditions, using Bonferroni corrections to address the problem of multiple comparisons. Effect sizes were calculated as Z / √ (number of observations.

ERPs. Cluster-based permutation tests[50,51] were conducted to test for effects of a) condition on mean amplitude and b) handedness on condition difference mean amplitude. This approach is designed to take into account the problem of multiple comparisons and data dependency in the statistical testing procedure. Potential condition differences (i.e., differences in the mean amplitude between the coherent and incoherent conditions) were examined separately for left- and right-handers. Potential handedness differences were examined by comparing the coherent minus incoherent mean amplitude difference observed in right- versus left-handers. In all instances, separate tests were conducted for the early and late time windows. For all tests, the number of permutations was set at 1000. Clusters of significant electrodes were built on the basis of spatial adjacency and significance thresholds exceeding $p < 0.01$. All electrode values within a cluster were required to have the same sign[52] (i.e., positive or negative). The observed cluster with the largest mass (i.e., sum of all values within the cluster) was compared against the critical cluster value at the 99th percentile of the null distribution.

Correlations. Correlation analyses were conducted to investigate the potential relationship between observed ERP activity and behavioural measures of vection in the coherent condition. After the ERP analyses identified the largest cluster of electrodes showing a significant mean amplitude difference between the coherent and incoherent conditions, the coherent condition mean amplitude values in the cluster electrodes were extracted. These were averaged together to give the cluster mean amplitude for the coherent condition. To enhance statistical power, the data for left- and right-handers were pooled. Spearman's rho correlations, with Bonferroni-corrections for multiple comparisons, were conducted to quantify the relationship between the cluster mean amplitude and each behavioural measure of vection. Separate analyses were conducted for early and late windows.

Results

Behavioural measures of vection

A summary of the behavioural data is presented in Table 1. Overall, stronger vection was experienced in the coherent condition, compared to the incoherent condition, for both left- and right-handers. Specifically, more vection present trials, shorter onset latencies, longer vection durations, and higher strength scores were reported in the coherent condition. The behavioural measures of vection each showed relatively large variability, as is indicated by the interquartile ranges (see Table 1). All participants reported experiencing vection in the coherent condition. As vection was rarely present in the incoherent condition (median number of trials: 4.5 for left-handers, 4 for right-handers), measures of onset latency, duration, and strength were derived from very few trials. Consequently, statistical analyses comparing behavioural measures in the coherent versus incoherent condition were not conducted. Statistical contrasts comparing left- and right-handers found no significant differences in any behavioural measure of vection, in either the coherent or the incoherent condition.

Table 1. Behavioural measures of vection. Median values (interquartile range) and statistical results from left- vs. right-hander comparisons, in coherent and incoherent conditions. No significant differences were observed between the two groups. All participants reported vection perception in the coherent condition, whereas only a few subjects reported vection perception in the incoherent condition. Further, the vection experienced in the incoherent condition had longer onset latencies, shorter durations, and weaker subjective strength reports, when compared to the vection experienced in the coherent condition. *Z* = z-statistic, *p* = p-statistic, and *r* = effect size

				Statistics		
		Left-handers	Right-handers	*Z*	*p*	*r*
Vection presence	Coherent	48 (6)	47 (6.5)	1.02	0.31	0.13
(max = 50)	Incoherent	4.5 (15)	4 (12)	-0.11	0.92	-0.01
Onset latency	Coherent	6.30 (4.61)	5.56 (4.62)	-0.26	0.80	0.03
(sec)	Incoherent	11.29 (9.43)	12.66 (8.51)	-0.85	0.39	-0.11
Duration	Coherent	12.62 (6.53)	14.29 (6.26)	-0.41	0.68	-0.05
(sec)	Incoherent	4.56 (5.74)	3.86 (7.02)	0.16	0.87	0.02
Strength	Coherent	5 (3)	5.5 (4)	-1.39	0.16	-0.17
(0 to 10)	Incoherent	0 (0)	0 (0)	-0.09	0.93	-0.01

Event related potentials (ERPs)

Following motion onset, two clear ERP peaks were observable in coherent and incoherent conditions, in both left- and right-handers (Fig. 1a, for example grand average ERPs in electrodes Cz and Oz). A general pattern of fronto-central negativity and parieto-occipital positivity was observed during the first peak, around 160 – 220 ms after motion onset (Fig. 1b). During the subsequent peak, around 260 – 300 ms, this pattern reversed in the coherent condition, with fronto-central positivity and parieto-occipital negativity being observed. The same peak in the incoherent condition was characterised by central positivity and surrounding negativity (Fig. 1b). In general, larger amplitudes were observed in the incoherent condition, in both left- and right-handers. As a group, left-handers exhibited larger amplitudes than right-handers.

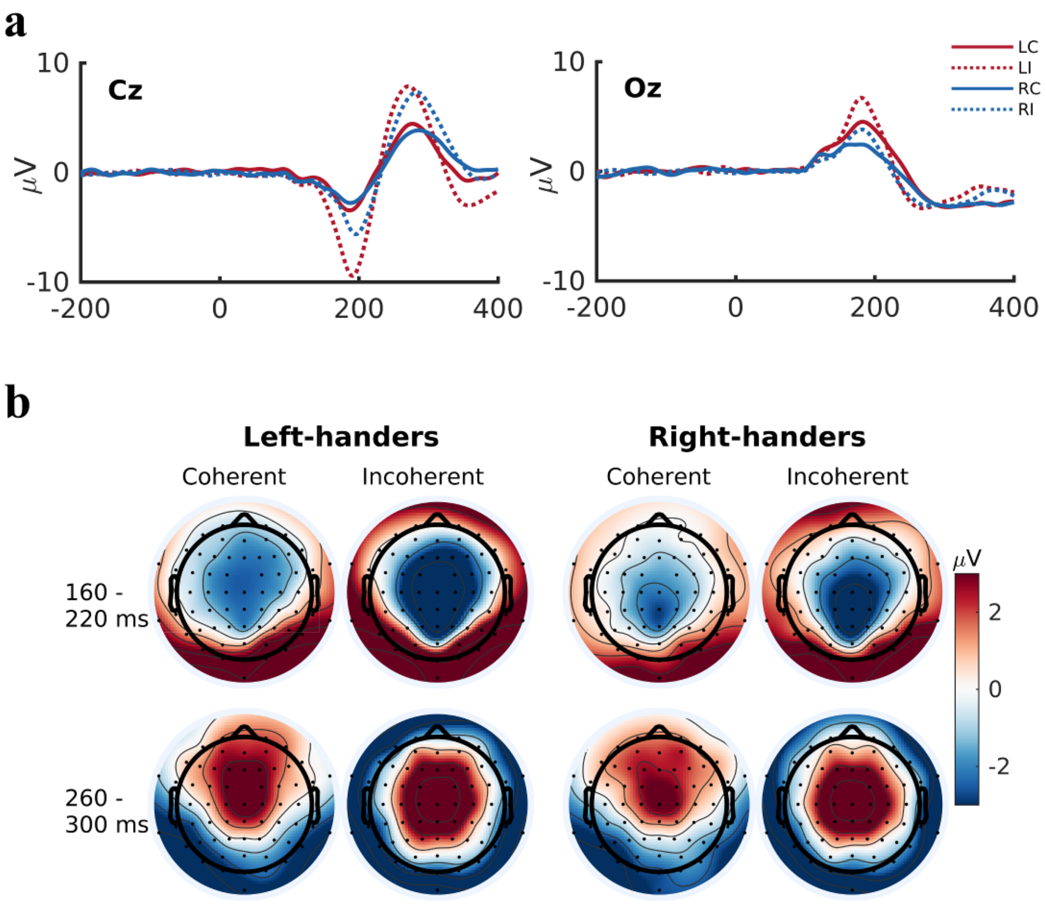

Figure 1

Overview of grand average ERP data. Panel a depicts the grand average ERP waveforms in example electrodes Cz and Oz. Two clear peaks were observed across almost all electrodes following motion onset: an early peak around 160 – 220 ms and a later peak around 260 – 300 ms. LC = left-handers coherent, LI = left-handers incoherent, RC = right-handers coherent, RI = right-handers incoherent. Panel b presents a topography of the mean amplitude values that were obtained in the early and late windows in the coherent and incoherent conditions, for left- and right-handers respectively. In both conditions, the early window was characterised by a pattern of fronto-central negativity (blue) and parieto-occipital positivity (red). This pattern reversed in the later window, with frontal positivity and parieto-occipital negativity in the coherent condition and a more central positivity with surrounding negativity in the incoherent condition. In general, larger amplitudes were observed in the incoherent condition and amongst the left-hander group.

Coherent versus incoherent

Mean amplitude differences in the coherent versus the incoherent condition were assessed using cluster-based permutation tests in the early (160 - 220 ms) and late windows (260 – 300 ms), for left- and right-handers respectively (Fig. 2). In each case, significant differences were observed in multiple electrode clusters. The largest cluster (defined by the summed mass) exceeding a threshold of $p < 0.01$ is reported.

Left-handers, early window. The largest cluster of electrodes exhibiting a significant condition difference was centrally located, centring around electrodes Cz/CPz and extending into both frontal and parietal electrodes (Fig. 2a). The cluster comprised electrodes showing a decreased mean amplitude in the coherent relative to the incoherent condition (Fig. 1b). Source localization analysis identified condition differences in estimated source activity across several brain regions. These regions include bilateral cingulate gyrus (mid/anterior and posterior divisions, and the cingulate sulcus visual (CSv) area); bilateral retrosplenial cortex; bilateral precuneus; sensorimotor regions (supplementary motor area, superior frontal gyrus, and pre- and post-central gyri); visual regions (bilateral cuneus, lateral occipital cortex, and occipital pole, and right intracalcarine cortex/V1); parieto-occipital regions (bilateral parietal lobule, right angular gyrus and supramarginal gyrus); frontal regions (right middle frontal gyrus and left inferior frontal gyrus); right middle temporal gyrus; and bilateral posterior insular/PIVC regions (left: parietal operculum including OP1/OP2, planum temporale, insular cortex; right: parietal operculum and planum temporale) (Fig. 3a). The maximum difference was found in the mid/anterior division of the cingulate gyrus.

Right-handers, early window. Similar to the left-handers, the largest cluster of electrodes showing a significant condition effect was centrally-located, stretching from parietal to centro-frontal electrodes (Fig. 2a). The cluster contained fewer electrodes and extended slightly less frontally when compared to the cluster observed in the left-hander group. Again, the cluster comprised electrodes showing a smaller mean amplitude in the coherent condition (Fig. 1b). Source localization analysis revealed condition differences in estimated source activity in several brain regions, including: bilateral cingulate gyrus (mid/anterior and posterior divisions, and area CSv); bilateral retrosplenial cortex; bilateral precuneus; bilateral sensorimotor precentral gyrus; visual regions (bilateral intracalarine cortex/V1, lateral occipital cortex, and right cuneus); parieto-occipital regions (bilateral parietal lobule, angular gyrus, and right supramarginal gyrus); and posterior insular/PIVC regions (left: planum temporale, insular cortex; right: planum temporale, insular cortex, parietal operculum, Heschel's gyrus/OP2) (Fig. 3b). The maximum difference was observed in the posterior division of the cingulate gyrus.

Left-handers, late window. The largest cluster of electrodes showing a significant condition difference was again centrally located, this time extending less frontally and more into parietal electrodes (Fig. 2b). Once more, the cluster comprised electrodes showing a smaller mean amplitude in the coherent, relative to the incoherent, condition. Source localization analysis identified significant condition differences in estimated source activity in bilateral posterior cingulate gyrus/retrosplenial cortex/precuneus and in bilateral mid/anterior cingulate gyrus (Fig. 4a). The maximum difference was located in the posterior cingulate gyrus/retrosplenial cortex.

Right-handers, late window. Again similar to the left-handers, the largest cluster showing condition differences was centrally located, with effects spreading into fronto-central and parietal electrodes (Fig. 2b). A smaller mean amplitude was observed across the cluster in the coherent condition. The source localization analysis revealed significant condition differences in estimated source activity in bilateral posterior cingulate gyrus/retrosplenial cortex/precuneus, right superior parietal lobule, left precentral gyrus, left postcentral gyrus, and left parieto-operculum/insular cortex (Fig. 4b). The maximum difference was located in the precuneus.

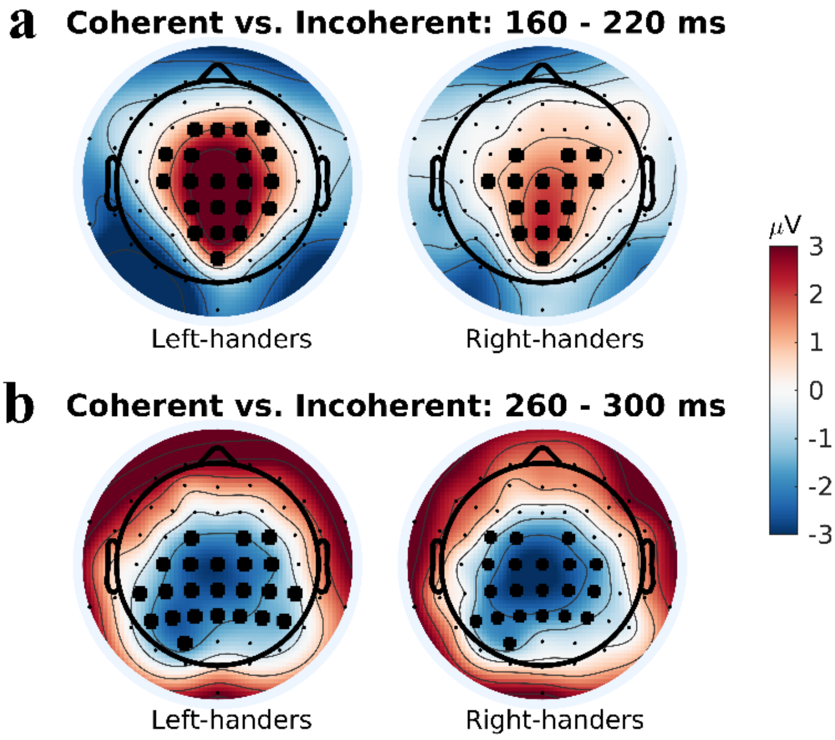

Figure 2

Mean amplitude in the coherent versus the incoherent condition. Cluster-based permutation tests were conducted to identify clusters of electrodes showing a significant difference in mean amplitude between the coherent and incoherent conditions in the early (160 – 220 ms) and late (260 – 300 ms) windows, for left- and right-handers respectively. The largest cluster of electrodes showing significant mean amplitude differences between the two conditions are indicated by large black dots over the respective electrode positions. For illustration purposes, condition differences are plotted as coherent mean amplitude minus incoherent mean amplitude, resulting in a net positive mean amplitude difference in the early window (red) and a net negative mean amplitude difference in the late window (blue). Panel a depicts the results in the early window for left- and right-handers. In both groups, a central cluster of electrodes, extending from parietal to frontal regions, exhibited significant condition differences, with attenuated mean amplitudes observed in the coherent relative to the incoherent condition. Panel b depicts the results in the late window for left- and right-handers. In both groups, a central cluster of electrodes, extending into centro-parietal regions, exhibited significant condition differences, with attenuated mean amplitudes observed in the coherent versus the incoherent condition.

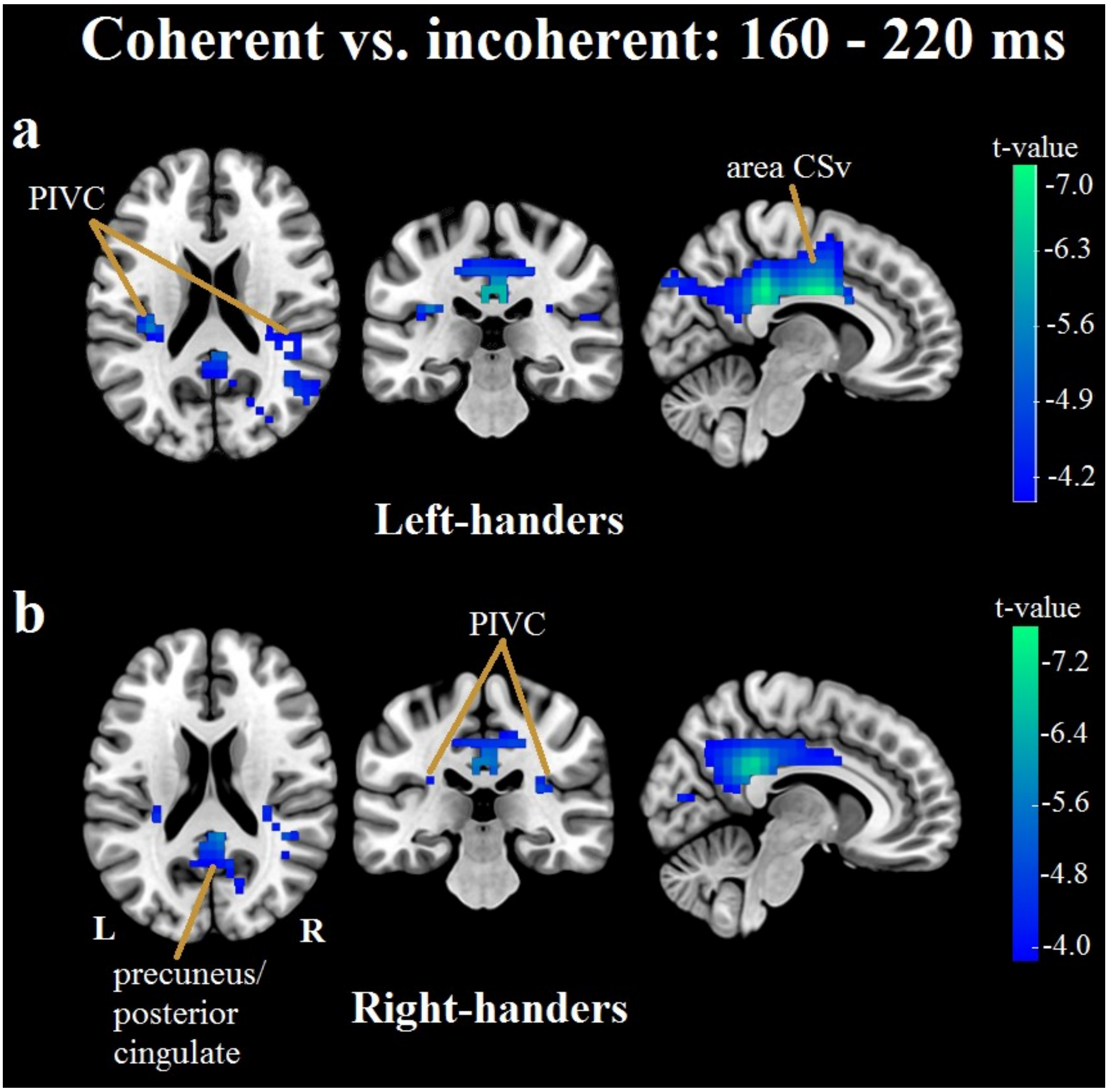

Figure 3

Visualisation of results from source localization analyses contrasting the estimated generators in the coherent versus the incoherent condition in the early (160 – 220 ms) window. In both left- and right-handers, estimated source activity differed across a large network consisting of the cingulate (including the cingulate sulcus visual (CSv) area), retrosplenial cortex, precuneus, sensorimotor, visual, parieto-occipital, frontal, and posterior insular/PIVC regions. Estimated source activity modulations in the cingulate, precuneus, and posterior insular/PIVC regions are depicted for left-handers (Panel a) and right-handers (Panel b). While left-handers exhibited bilateral activity in posterior insular/PIVC regions, right-handers showed hemispheric asymmetry with more activity in the right posterior insular/PIVC regions.

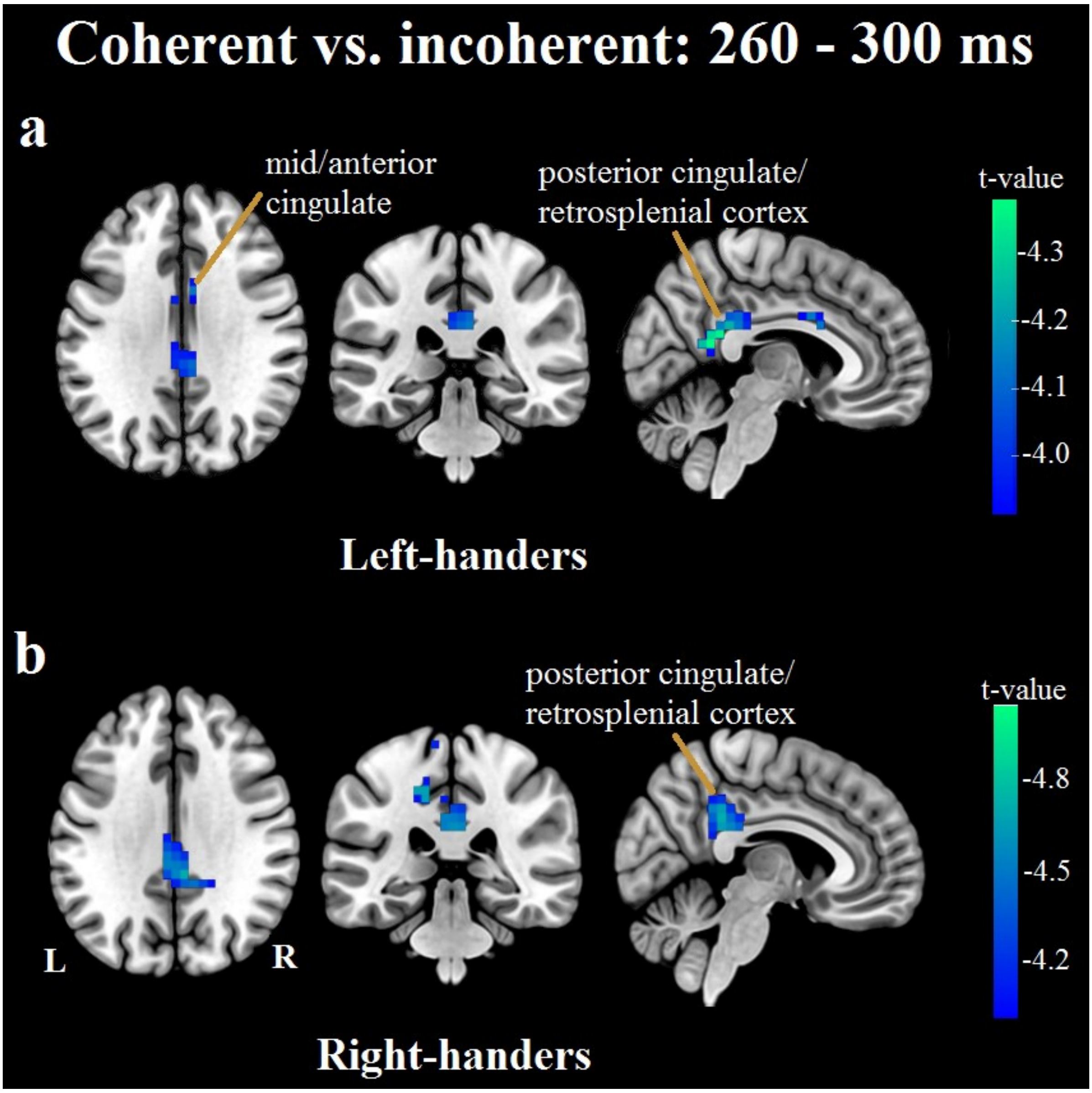

Figure 4

Visualisation of results from source localization analyses contrasting the estimated generators in the coherent versus the incoherent condition in the late (260 – 300 ms) window. In left-handers (Panel a), estimated source activity modulations were observed in the posterior cingulate/retrosplenial cortex/precuneus, and the mid/anterior cingulate. In right-handers, estimated source activity modulations were identified in the posterior cingulate/retrosplenial cortex/precuneus, superior parietal lobule, pre- and post-central gyri, and (left) parieto-operculum/insular cortex. Panel b depicts the estimated source activity differences in the posterior cingulate/retrosplenial cortex/precuneus observed in right-handers.

Right-handers versus left-handers

Differences between left- and right-handers were examined by comparing the coherent minus incoherent mean amplitude difference between the two groups. Again, significant differences were assessed by means of cluster-based permutation tests in the early and late windows and the largest clusters exceeding a threshold of p < 0.01 are reported.

Early window. A cluster of electrodes showing significant differences between left- and right-handers was centrally located, extending partially into fronto-central and centro-parietal electrodes (Fig. 5). This cluster reflects a larger mean amplitude difference in left-handers as compared to right-handers. More specifically, while both left- and right-handers showed a smaller amplitude in the coherent compared to the incoherent condition, this difference was greater for left-handers. Source localization analysis found significant differences in estimated source activity bilaterally in area CSv, extending along the mid/anterior cingulate and into the supplementary motor cortex (Fig. 6).

Late *window.* No significant differences were observed between the two groups.

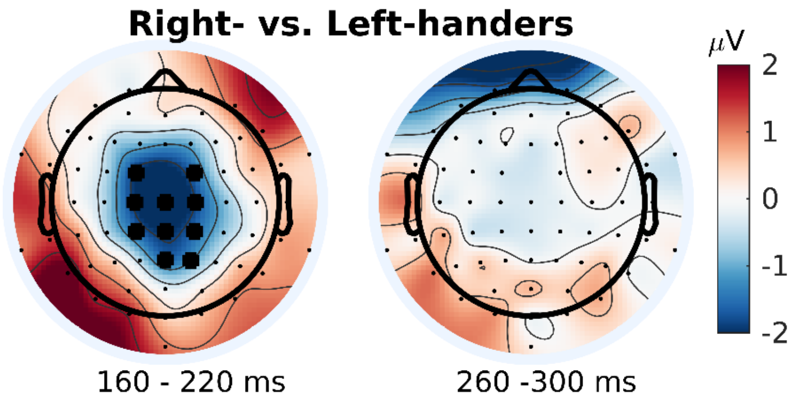

Figure 5

Condition difference (i.e., coherent mean amplitude minus incoherent mean amplitude) in right- versus left-handers. Cluster-based permutation tests were conducted to identify clusters of electrodes showing a significant condition difference between left- and right-handers in the early (160 – 220 ms) and late (260 – 300 ms) windows. For illustration purposes, condition differences between the two groups are plotted as right-hander condition difference minus left-hander condition difference. In the early window, a central cluster of electrodes (indicated by large black dots over respective electrode positions) exhibited a significant condition difference between the two groups, reflecting a larger mean amplitude difference in left- versus right-handers. That is, although both groups exhibited smaller mean amplitudes in the coherent relative to the incoherent condition, the difference between conditions was larger for left-handers. No significant differences were observed in the late window.

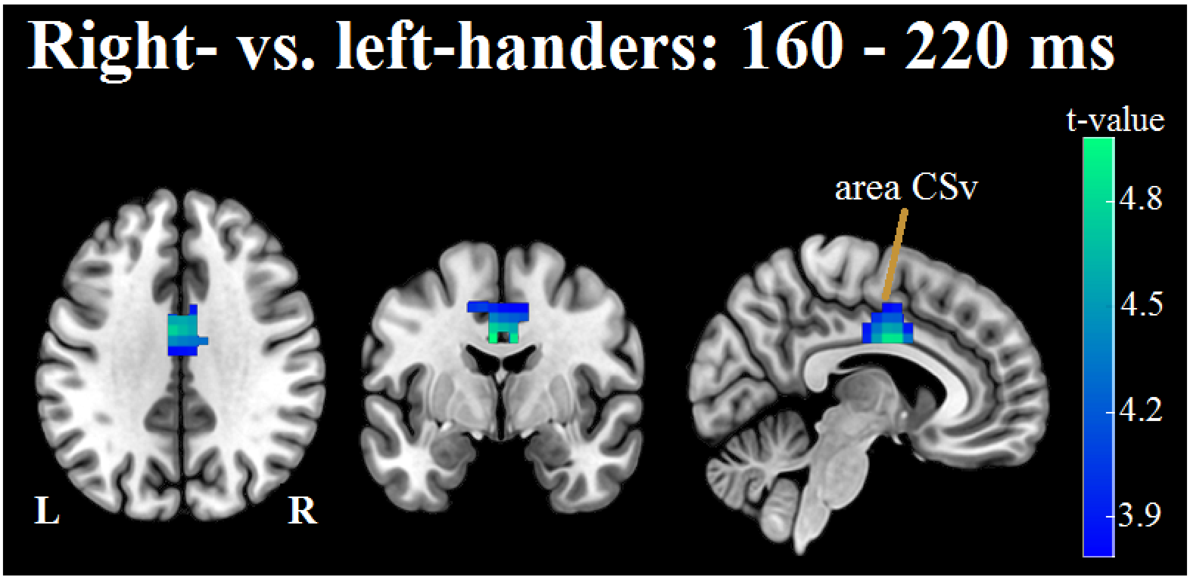

Figure 6

Visualisation of results from source localization analysis comparing the differences in estimated source activity between conditions in right- versus left-handers, during the early (160 – 220 ms) window. Results revealed that the estimated source activity exhibited in the coherent minus the incoherent condition differed between left- and right-handers primarily in area CSv.

Behaviour-EEG correlations

The potential relationship between cluster mean amplitude and each behavioural measure of vection in the coherent condition was examined using Spearman's rho correlations, with separate tests for early and late windows.

Early window. No significant correlations were observed between cluster mean amplitude and vection presence ($\rho(55) = 0.11$, $p = 0.42$), onset latency ($\rho(55) = -0.04$, $p = 0.75$), or duration ($\rho(55) = 0.09$, $p = 0.51$). A moderate correlation was observed between mean amplitude and vection strength ($\rho(55) = -0.31$, $p = 0.018$), however, this failed to reach statistical significance after correction for multiple comparisons.

Late window. No significant correlations were observed between cluster mean amplitude and vection presence (ρ(55) = -0.05, p = 0.71), onset latency (ρ(55) = 0.05, p = 0.72), vection duration (ρ(55) = 0.01, p = 0.92), or vection strength (ρ(55) = -0.06, p = 0.65).

Discussion

The present study used ERPs and source localization (eLORETA) to investigate the early neural processing of coherent vection-compatible visual motion stimulation against that of incoherent vection-incompatible motion stimulation in left- versus right-handers. The behavioural results show that prolonged exposure to the coherent stimulation resulted in strong and reliable vection perception across participants, whereas prolonged exposure to the incoherent stimulation produced only infrequent reports of a relatively weaker vection. Onset of both coherent and incoherent motion stimulation generated ERP responses, with clear early (160 – 220 ms) and late (260 – 300 ms) peaks. In both windows, ERP analyses revealed reduced mean amplitudes in the coherent, relative to the incoherent, condition over predominantly central electrodes for both left- and right-handers (Fig. 2). In the early window, both left- and right-handers exhibited estimated source activity condition differences across a wide cortical network, including the cingulate and area CSv, the retrosplenial cortex, the posterior insula/PIVC, the precuneus, and visual, frontal and somatosensory regions (Fig. 3). In the late window, similar analyses identified estimated source activity differences primarily in the posterior cingulate/retrosplenial cortex/precuneus (Fig. 4). Comparison of left- and right-hander ERP activity in the early window found a greater mean amplitude difference between conditions amongst the left-hander group. Accompanying source localization analysis revealed that condition modulations of estimated source activity differed between left- and right-handers primarily in visual area CSv (Fig. 6). Despite these EEG differences, left- and right-handers reported comparable vection perception during prolonged motion stimulation exposure. Importantly, although vection was present and behaviourally measured in the current study, ERP and source localization findings are time-locked to motion onset, which occurs several seconds prior to vection onset. Thus, the reported ERP and source localization findings reflect the neural processes that occur *before* vection perception.

Prior ERP studies investigating pre-vection neural processes have emphasised two key findings: firstly, that motion onset of various movement patterns generates modulations of parieto-occipital P1/P2 and N2 components and secondly, that a tentative relationship exists between parieto-occipital N2 component amplitude and subjectively perceived vection strength/intensity[22–24]. Although parieto-occipital ERPs were observable in the present study (see Fig. 1b for the ERPs obtained at electrode Oz), our findings are concerned with the ERPs obtained over central electrode sites, as our analyses indicated that this cluster of electrodes exhibited the largest mean amplitude condition differences. The spatial discrepancy between our findings and those of previous studies may be partially attributed to our choice of control (i.e., incoherent) stimulation. In contrast to previous studies, which compared different centre-surround motion patterns[22,23] or coherent versus random motion[24], we attempted to match our vection-compatible and control stimuli for lower-level properties, including global mean velocity. In this way, we attenuated (but did not eliminate) ERP effects due to physical stimulus differences, which may have reduced the strength of ERP condition differences over parieto-occipital electrodes in contrast to previous studies. Moreover, unlike previous studies[22–24], we employed large-field motion stimulation that covered the entire field-of-view, resulting in more salient motion and possibly more robust, extensive recruitment of optic flow processing networks. Although previous studies have reported a correlation between N2 component amplitude and subjective vection strength/intensity[22–24], our results proved inconclusive on this matter, identifying a moderate ($\rho = -0.31$) but non-significant correlation in the coherent condition between mean cluster amplitude in the early (160 – 220 ms) window and reports of subjective vection strength. Since this correlation was observed during coherent stimulation, just 160 – 220 ms after motion onset, it is possible that it reflects general motion detection and the processing of coherent versus incoherent motion rather than a specific distinction of vection-compatible (as opposed to vection-incompatible) motion stimulation. Further research is required to disambiguate the relationship between the pre-vection N2 component and the subsequent subjective experience of vection strength/intensity.

Comparison of the ERPs evoked by coherent versus incoherent stimulation revealed consistent, relatively attenuated mean amplitudes in response to the vection-compatible coherent motion during both early and late windows. Accompanying source localization analyses, contrasting the estimated source activity in both conditions, identified largely distinct modulation patterns in the early and late windows. In the early window, estimated source activity differences were widespread across the cortex, including visual, sensorimotor, and multisensory vestibular networks. For both left- and right-handers, the strongest and most extensive condition modulations were observed in the cingulate cortex, which is part of the multisensory cortical vestibular network[32,33]. The cingulate has previously be found to prefer naturalistic self-motion over object-motion[13] and has also been linked to vection perception[4,5,9]. Moreover, the bilateral cingulate sulcus visual (CSv) area has consistently been shown to be active during visual motion stimulation, only if the stimulation is self-motion compatible[53–55]. Notably, the identified modulations in left- and right-handers are located predominantly in mid and posterior cingulate regions, extending ventrally towards the border of the corpus callosum. Intracortical electrical stimulation of epilepsy patients in these regions was previously found to evoke subjective vestibular, interoceptive, somatosensory, and visual sensations[56].

During the early window, left- and right-handers also exhibited condition modulations of estimated source activity in the posterior insular/PIVC regions, which are core regions in the multisensory cortical vestibular network[32,33]. In line with previous findings demonstrating a thalamo-cortical hemispheric lateralization of the multisensory vestibular network during vestibular stimulation[28–34], right-handers here exhibited a hemispheric asymmetry, with greater estimated source activity modulations in the right posterior insular/PIVC regions during visual motion stimulation. In contrast, left-handers exhibited bilateral estimated source activity modulations, with no asymmetry towards left posterior insular/PIVC regions during visual motion stimulation. This absence of left hemispheric dominance may reflect a weaker, more variable handedness preference amongst the left-handers. Indeed, as a group the left-handers exhibited more variable handedness laterality quotients (i.e., handedness scores) than the right-hander group (see Methods section for details). For both groups, estimated source activity modulations in the posterior insular regions included the planum temporale and parietal operculum, which have both previously been shown to respond more strongly to coherent/egomotion-compatible versus incoherent/egomotion-incompatible visual stimulation[54,57].

In the late window, estimated source activity differences between the coherent and incoherent conditions were predominantly located in the posterior cingulate/retrosplenial cortex/precuneus for both left- and right-handers. The retrosplenial cortex is involved various aspects of spatial navigation and memory[58–60], and has been found to be involved in the computation of heading direction during optic flow[61] and active navigation[62]. Moreover, it is thought to be critically involved in the translation of information between allocentric (world-centred) and egocentric (self-centred) spatial reference frames[46,59,63–68]. Relatedly, the precuneus is thought to play a role in developing and maintaining concurrent egocentric and allocentric spatial reference frames[46,69]. There is also evidence to suggest that the posterior cingulate and retrosplenial cortex both contribute to our sense of self-location, with the posterior cingulate being particularly involved in the integration of neural representations of self-location and body ownership[70]. Altogether, our finding of condition modulations in these regions indicates heading computation differences between the two conditions, most likely due to stronger heading information in the vection-compatible coherent condition. Moreover, it suggests that vection-compatible coherent motion and vection-incompatible incoherent motion interact differently with the network underlying egocentric and allocentric spatial reference frames.

Our comparison of ERP condition differences in left- versus right-handers during the early window revealed a larger mean amplitude difference between coherent and incoherent stimulation in the left-handers. Accompanying source localization analysis in the same window identified group differences primarily in area CSv. It is now well established that area CSv not only prefers egomotion-compatible visual stimulation, but that it also shows suppressed or absent responses to egomotion-incompatible stimulation[13,53,54,71,72]. This raises the question of whether the larger ERP condition difference exhibited by the left-handers, partly reflects a greater suppression of CSv activity in response to incoherent versus coherent motion, as compared to that observed in the right-handers. Importantly, left- and right-handers reported comparable vection perception within both conditions, suggesting that the observed group differences in EEG activity are not due to one group experiencing more/less egomotion-compatibility in the coherent and/or incoherent condition, as compared to the other group.

In addition to visual egomotion stimulation, area CSv is also strongly responsive to vestibular stimulation[73,74], making it a candidate location for the integration of visual and vestibular information related to self-motion[55,73]. Further, not only does area CSv receive afferent input from the vestibular system[73], but functional and diffusion MRI indicate connectivity between area CSv and both ipsi- and contra-lateral posterior insular cortex (PIC)[75]. In recent years, evidence has emerged to suggest that the PIVC responds to vestibular input and is suppressed by visual motion stimulation whereas the posteriorly adjacent PIC comprises a distinct multisensory region responsive to both visual and vestibular inputs[34,76]. Due to the limited spatial resolution of EEG source localization methods, the present study does not attempt to distinguish between these two areas and rather refers to condition differences in the general posterior insular/PIVC region. Notably, the observed condition differences in this posterior insular/PIVC region are bilateral in left-handers and asymmetrical towards the right-hemisphere in right-handers, and occur in the same time window as the observed group differences in area CSv. Based on the outlined connectivity between these regions, a question arises about whether (and how) the handedness-dependent condition differences in the posterior insular/PIVC region might relate to the group differences in area CSv. We speculate that different handedness-dependent activity patterns in the posterior insula during coherent versus incoherent visual stimulation might result in differential afferent (and/or feedback) signals with area CSv, thus resulting in the observed EEG group differences. Given the comparable perceptual reports from left- and right-handers such connectivity differences would appear to be behaviourally insignificant, at least in the context of the present study. Addressing these speculations will require future research that takes advantage of the enhanced spatial resolution of MRI and EEG/MRI connectivity methods.

A possible limitation of the present study is that it does not address the potential contribution of torsional eye movements to the observed effects. Although participants maintained central fixation, both conditions included continuous roll motion capable of triggering mild torsion. As we did not measure torsion, we cannot exclude the possibility that the global motion in the incoherent condition resulted in weaker, less frequent torsion relative to that in the coherent condition. Although we did not observe condition differences in oculomotor-specific regions, area CSv is also thought to be involved in the integration of oculomotor and visual motion signals related to self-motion[45,77]. As such, it is possible that torsional eye movements contribute in small part to our condition difference findings.

In conclusion, we observed that vection-compatible motion stimulation evoked consistently attenuated central ERPs, relative to incoherent control stimulation, for both left- and right-handers. Early ERP differences were accompanied by estimated source activity modulations across a large cortical network comprising visual, sensorimotor, and multisensory vestibular regions, whereas modulations accompanying later ERP differences were limited to the posterior cingulate/retrosplenial cortex and precuneus. In contrast to right-handers, left-handers exhibited a larger ERP condition difference. This was accompanied by group differences in the cingulate sulcus visual (CSv) area, suggesting that handedness may influence both ERP and area CSv responses to vection-compatible and vection-incompatible visual motion stimulation.

Declarations

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Author contributions

MM, TB, and MD contributed to the study design. MM collected and analysed the data. All authors contributed to and approved the manuscript.

Data availability statement

The datasets generated and analysed during the current study are not publicly available due to the constraints of the ethical approval but are available from the corresponding author on reasonable request.

Competing interests statement

The author(s) declare no competing interests.

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3. GENERAL DISCUSSION

This thesis had two major aims: 1) to apply EEG techniques to the study of vection perception and 2) to examine the potential lateralization of vection processing in left- and right-handers. To this end, two experimental studies were conducted. The first study investigated the behavioural characteristics and neural oscillations associated with vection perception in left- and right-handers. The second study investigated the temporal activation of the vection network by vection-compatible visual motion stimulation and examined the lateralization of these processes in left- versus right-handers, in view of the hemispheric lateralization of cortical vestibular processing reported in earlier imaging studies (Dieterich et al., 2003; Janzen et al., 2008; Schlindwein et al., 2008; zu Eulenburg et al., 2012). The following sections briefly summarise i) the experimental paradigm and ii) main findings from both studies, discussing iii) the insights gained by studying vection perception with EEG, iv) the relationship between handedness, lateralization of cortical multisensory vestibular processing, and vection perception, v) future directions in vection research, and vi) the functional significance of vection.

3.1 Summary of the experimental paradigm

The two studies presented in this thesis required an experimental paradigm that a) generated stable, compelling vection perception and b) included a control stimulus that matched the low-level visual properties contained in the vection-inducing stimulus, but which rarely produced vection perception. This led to the development of a coherent visual motion stimulus and an incoherent/control visual motion stimulus. Developing these motion stimuli was a non-trivial, integral part of this thesis, allowing the subsequently conducted studies to identify vection-related brain activity while attenuating (but not eliminating) confounding effects due to stimulus differences or general motion processing. EEG was recorded while the motion stimuli were presented using a custom-built experimental apparatus. Vection onset, offset, and direction were reported in real time via button presses and perceived vection strength was verbally reported at the end of each trial. This allowed the calculation of behavioural measures of vection (i.e., vection presence, onset latency, vection duration, and perceived vection strength) on a trial-by-trial basis. Both studies in this thesis found that prolonged exposure to the coherent stimulation produces strong and reliable vection perception across participants, whereas the incoherent stimulation leads to infrequent, relatively weaker vection perception. Specifically, the vection experienced under incoherent stimulation occurred less frequently, had longer onset latencies, shorter durations, and weaker strength compared to the vection experienced under coherent stimulation. Consequently, this discussion refers to the coherent stimulation as vection-compatible and the incoherent stimulation as vection-incompatible.

3.2 Summary of findings

The first study in this thesis (McAssey et al., 2020, Chapter 2.1) investigated the behavioural characteristics and neural oscillations associated with vection perception in left- and right-handers. The study found no differences between left- and right-handers on behavioural measures of vection (i.e., presence, onset latency, duration, and strength). Fast Fourier Transform (FFT) analyses revealed a decrease in alpha power during vection-compatible, relative to vection-incompatible, motion stimulation in both left- and right-handers. Notably, the topography of this effect was handedness-dependent, with left-handers showing a decrease over left lateralized centro-parietal electrodes and right-handers showing a decrease over bilateral midline centro-parietal electrodes. Similar analyses found no effects in the theta or beta bands. Further time-frequency analyses, time-locked to vection onset, revealed a decrease in alpha power around the time of vection onset and a relative increase in alpha power during ongoing vection perception, which was comparable in left- and right-handers. Altogether, this study revealed that vection-compatible visual motion is associated with centro-parietal alpha power decreases, with the exact topography of these decreases varying in a handedness-dependent manner. Further, despite differences in where vection-related activity is observed, left- and right-handers experience similar vection perception. Lastly, changes in alpha activity appear to reflect the dynamics of vection perception, indexing vection onset and the maintenance of ongoing vection perception.

The second study in this thesis (Chapter 2.2) investigated the temporal activation of the vection network by vection-compatible stimulation and examined the lateralization of these processes in left- versus right-handers. This involved comparison of the event-related potentials (ERPs) evoked by the onset of vection-compatible versus vection-incompatible motion, and their respective estimated neural generators. Importantly, although vection was present and behaviourally measured in this study, all EEG analyses were time-locked to motion onset, which occurred several seconds prior to vection onset. Thus, the EEG findings reflected the neural processes that occur *before* vection perception. In both left- and right-handers, vection-compatible motion evoked central ERPs, with relatively attenuated mean amplitudes in an early (160 – 220 ms) and a late (260 – 300 ms) time window. In the early window, comparison of the estimated source activity during vection-compatible versus vection-incompatible motion found that both left- and right-handers exhibited differences across a wide cortical network, including the cingulate and area CSv, the retrosplenial cortex, the posterior insula/PIVC, the precuneus, and visual, frontal and somatosensory regions. Notably, differences in the posterior insular cortex/PIVC were bilateral for left-handers but showed a hemispheric asymmetry towards the right-hemisphere in right-handers. In the late window, both left- and right-handers exhibited estimated source activity differences primarily in the posterior cingulate, retrosplenial cortex, and precuneus. Comparison of left- and right-hander ERP activity in the early window revealed a greater mean amplitude difference between vection-compatible and vection-incompatible motion in left-handers and estimated source activity differences between the two groups in the CSv area. Despite these differences in EEG activity, left- and right-handers subsequently went on to experience comparable vection perception. Altogether, this study revealed that vection-compatible visual motion stimulation evokes consistently attenuated central ERPs and interacts differently with visual, sensorimotor, and multisensory vestibular networks, relative to vection-incompatible stimulation. Further, the study demonstrates that handedness may influence ERP responses and area CSv activity in response to vection-compatible versus vection-incompatible visual motion stimulation.

3.3 Insights gained by studying vection perception with EEG

By examining various properties of the EEG signal, the two studies in this thesis made several novel observations about the neural mechanisms involved in the processing of vection-compatible visual motion stimulation and vection perception. The following sections briefly discuss the implications of these findings, focusing on a) the temporal dynamics of vection perception, b) the relationship between alpha oscillations and vection perception, and c) the remaining open questions that should be addressed in future research.

a) The temporal dynamics of vection perception

Vection perception typically develops over a period of several seconds (Brandt et al., 1973; Dichgans & Brandt, 1978) and tends to alternate with periods of object-motion perception, even under constant visual motion stimulation (Dichgans & Brandt, 1978; Kleinschmidt et al., 2002; Thilo et al., 2003). Further, vection perception may persist for a short period beyond the cessation of visual motion stimulation (Becker-Bense et al., 2012; Dichgans & Brandt, 1978). Altogether, this points to the fact that, in context, vection perception is a temporally dynamic phenomenon. Moreover, individual differences in onset latency and vection duration (Brandt et al., 1973; Dowsett et al., 2017; Kennedy et al., 1996) demonstrate that the temporal dynamics of vection perception are largely variable between individuals. In contrast to other neuroimaging methods (e.g., PET and fMRI), EEG offers extremely high temporal accuracy and may therefore be used to track the relationship between continuous changes in brain activity and the temporal dynamics of vection perception. The sections below summarise the findings this thesis made in this regard.

Pre-vection processes

Egomotion-compatible optic flow is a prerequisite for (visually-induced) vection perception. Yet, the brain's initial response to such motion stimulation is rarely examined in vection studies, as vection itself is typically not present in this time frame. As a result, it is unclear if (and how) the early neural processes triggered by vection-compatible motion relate to the later emergence of vection perception. While these early processes are not vection-specific, they may be vection-relevant. For instance, many studies employ constant visual motion stimulation, meaning that the visual input at motion onset is identical to that at vection onset, making the early processing of such stimulation inherently related (but not specific) to vection perception.

This thesis (Study 2, Chapter 2.2) examined the early neural responses triggered by vection-compatible versus vection-incompatible visual motion onset, finding that vection-compatible motion evokes relatively attenuated central ERPs. These ERP attenuations were observed just 160 - 220 ms and 260 – 300 ms after motion onset, indicating that the processing of vection-compatible and vection-incompatible motion differs even at very early processing stages. Further, the early processing of vection-compatible and vection-incompatible motion was found to differentially engage cortical visual, sensorimotor, and multisensory vestibular networks. Interestingly, with respect to cortical localization, several of the brain areas that responded differently to the onset of vection-compatible and vection-incompatible motion (e.g., the PIVC, CSv area, precuneus, and lateral occipital cortex) have previously been linked by PET and fMRI studies to optic flow parsing (Pitzalis et al., 2020) and vection perception (Berti & Keshavarz, 2021; see also Table 2 Chapter 1.4). This suggests that the networks responsible for vection perception and the distinction of object- versus self-motion, are involved in the early processing of vection-(in)compatible visual motion, several seconds prior to the emergence of vection perception.

As vection is not present at the time of these ERP and source activity effects, a question arises about what these differences actually reflect. Vection-inducing and non-vection-inducing motion stimuli inherently differ in their visual properties; otherwise, both stimuli would generate the same perceptual experience (i.e., vection or no vection). Consequently, one possible explanation for the observed EEG effects is that the vection-compatible and vection-incompatible stimuli trigger different neural processes because of differences in their respective low-level visual properties. Although this possibility cannot be excluded, two factors provide evidence against such an interpretation. Firstly, the vection-compatible and vection-incompatible stimuli were matched for low-level visual properties (e.g., number of dots, luminance, global mean velocity etc.), which likely reduced (but did not eliminate) effects due to visual property differences between the two stimulation types. Secondly, the ERP effects were observed over predominantly central electrode sites, whereas differences relating to low-level visual properties would be expected primarily over occipital electrode sites.

A second, more plausible explanation is that the EEG effects reflect the initial detection and processing of visual motion, through which egomotion-compatibility is discriminated. This interpretation is supported by the observation that the retroinsular cortex/PIVC region and the CSv area both responded differently to vection-compatible (i.e., coherent) and vection-incompatible (i.e., incoherent) motion. Coherent optic flow is a strong indicator of egomotion and both of these regions have previously been shown to distinguish between coherent/egomotion-compatible and incoherent/egomotion-incompatible visual stimulation (Antal et al., 2008; Cardin & Smith, 2010; Pitzalis et al., 2020; Smith, 2021; Wall & Smith, 2008). Further, subsequent differences between vection-compatible and vection-incompatible motion were identified in the retrosplenial cortex, posterior cingulate, and precuneus. The retrosplenial cortex is involved in the computation of heading direction from optic flow (Diekmann et al., 2009), our sense of self-location (Guterstam et al., 2015), and the translation of information between allocentric (world-centred) and egocentric (self-centred) spatial reference frames (e.g., Burgess, 2008; Chiu et al., 2012; Gramann et al., 2010; Lin et al., 2015; Vann et al., 2009). Relatedly, the precuneus is thought to be involved in the development and maintenance of concurrent egocentric and allocentric spatial reference frames (Derbie et al., 2021; Gramann et al., 2010), while the posterior cingulate has been linked to our sense of self-location and the integration of self-motion and body ownership neural representations (Guterstam et al., 2015). Together, this indicates that the EEG effects also reflect a differential interaction of vection-compatible and vection-incompatible motion with the networks supporting egocentric and allocentric spatial reference frames.

Altogether, these findings demonstrate that visual motion onset initiates neural processes that are modulated by the egomotion-compatibility of the stimulation. These processes appear to reflect the discrimination of coherency/egomotion-compatibility and the engagement of optic flow parsing, vection perception, and ego-/allo-centric spatial reference frame networks. Although these processes are insufficient to induce vection, the discrimination of visual motion as egomotion-compatible is a prerequisite for the (later) generation of (visually-induced) vection perception, thus making such processes vection-relevant.

Vection-related processes

Using FFT analyses, this thesis revealed an association between vection-compatible visual motion stimulation and decreased centro-parietal alpha power (Study 1, Chapter 2.1). This effect was found by comparing the oscillatory activity observed during prolonged (i.e., 20 seconds) vection-compatible versus vection-incompatible stimulation. Behavioural data obtained during the motion stimulation showed that vection was almost always present in vection-compatible trials (i.e., 94 – 96% of trials) but rarely present in vection-incompatible trials (i.e., 4 – 8% of trials). Moreover, vection-compatible stimulation produced early and persistent vection (i.e., onset latency: ~5 – 6 seconds; duration: ~12 – 13 seconds), whereas vection-incompatible stimulation produced later, shorter vection perception (i.e., onset latency; ~10 – 12 seconds; duration: ~3 – 5 second). Thus, the observed decrease in alpha power occurred in the presence of vection perception. In other words, these findings demonstrate that prolonged vection-inducing visual motion stimulation is associated with decreased centro-parietal alpha power.

Vection-specific processes

Using time-frequency analyses, time-locked to vection onset, this thesis found tentative evidence that centro-parietal alpha activity indexes the dynamics of vection perception (Study 1, Chapter 2.1). Specifically, these analyses revealed that alpha power decreases around the time of vection onset and gradually increases during ongoing vection perception. It should be noted that although both left- and right-handers exhibited a clear decrease in alpha power around vection onset, this effect did not reach statistical significance in the right-hander group. Overall, these findings indicate that alpha activity may reflect vection dynamics, potentially providing a future objective marker of vection perception.

b) The relationship between alpha oscillations and vection perception

Alpha oscillations are a central feature of human brain activity and they have been linked with a broad range of cognitive functions (Clayton et al., 2018). For instance, alpha oscillations are thought to be involved in the active suppression of irrelevant sensory information, the regulation of perceptual temporal resolution, the alternation between periods of top-down prediction and bottom-up processing, the facilitation of communication across the brain, and the stability of visual processing (Clayton et al., 2018). The roles of alpha oscillations in vection perception are discussed below.

Role 1: transient alpha power decreases and the transition to vection perception

Studies of multi-stable perception provide evidence for a relationship between alpha oscillations and the stability of visual processing (Clayton et al., 2018). In particular, reductions of alpha power are thought to reflect the destabilisation of perceptual interpretations of ambiguous visual stimuli and the shifting of perception towards alternative interpretations (Mathes et al., 2010; Struber & Herrmann, 2002). In line with this evidence, both the present thesis (McAssey et al., 2020, Study 1, Chapter 2.1) and a study by

Harquel et al. (2020) observed a decrease in alpha power around the time of vection onset, which likely reflects the transition from object- to self-motion perception.

Notably, these transient decreases in alpha power began slightly before reported vection onset, most likely reflecting the temporal delay between the emergence of a conscious vection percept and the execution of the button press indicating vection presence. An alternative explanation is that the observed alpha power decreases actually reflect components of the mu motor rhythm related to the button press, especially since these effects were found over centro-parietal (McAssey et al., 2020, Study 1, Chapter 2.1) and sensorimotor cortex (Harquel et al., 2020). The mu rhythm is an oscillation found over sensorimotor cortex, with dominant frequencies in the 8 – 12 Hz and 15 – 25 Hz bands (Hari & Salmelin, 1997), thus overlapping with alpha and beta band frequencies. Importantly, Harquel et al. (2020) showed that power decreases in the low-mu/alpha range occur around the time of button presses indicating vection onset, but not around the time of identical button presses in a (no vection) control task. Thus, the observed reduction in alpha power cannot be attributed to button-press-related motor processing and is instead more likely to reflect the perceptual switch from object- to self-motion perception. It should be acknowledged, however, that this finding does not exclude the possibility that mu oscillations are involved in vection perception. Indeed, mu activity is associated with the translation of sensory information into motor processing (Pineda, 2005), making mu/alpha oscillations a candidate mechanism for distinguishing between object- and self-motion in order to facilitate appropriate motor responses (Berti & Keshavarz, 2021).

Role 2: increased alpha power facilitates vection perception

Alpha oscillations have been long been associated with the active suppression of irrelevant sensory processing (Clayton et al., 2018; Klimesch et al., 2007), with alpha power increases typically being reported in brain areas that are not task relevant (Klimesch et al., 2007). For example, when asked to attend to auditory stimuli over visual stimuli, participants demonstrate increased alpha power over parietal (i.e., visually associated) regions (Fu et al., 2001). Such evidence suggests that increasing alpha power during ongoing vection perception, observed in the present thesis (McAssey et al., 2020, Study 1, Chapter 2.1) and in the study by Harquel et al. (2020), likely reflects the inhibition of irrelevant sensory processing in order to maintain vection perception.

In the context of vection, irrelevant sensory processing might include, for example, visual signals indicating object-motion rather than self-motion and/or vestibular signals indicating an absence of self-motion. Interestingly, Harquel et al. (2020) found alpha power increases during ongoing vection perception when participants were upright but not when they were supine, despite identical visual motion stimulation in both positions. This finding is thought to reflect the fact that roll vection induces differing amounts of visual-vestibular conflict in upright and supine positions. That is, in contrast to a supine observer, an upright observer must additionally ignore information from the vestibular otolith organs indicating that the head is stationary with respect to gravity if they are to maintain roll vection perception. Indeed, stationary observers exposed to large-field visual motion stimulation in the roll plane (about the line of sight) have been found to experience an ambiguous perception of roll motion of the body with only a limited tilt relative to the gravitational field (Dichgans et al., 1972). Overall, the finding by Harquel et al. (2020) is congruent with evidence showing that greater inhibition requirements are associated with greater alpha power increases (Klimesch et al., 1999, 2000). Altogether, these findings indicate that alpha power increases facilitate the maintenance of vection perception by inhibiting irrelevant sensory processing, with greater alpha power increases reflecting greater inhibition requirements.

c) Studying vection perception with EEG: open questions

Based on the findings of this thesis, several new questions have emerged regarding the temporal dynamics of vection and the relationship between alpha oscillations and vection perception. Below is a short list of such questions, which should be addressed in future research.

1. *What neural processes are involved in the onset latency period?*

   The findings of this thesis demonstrate that the onset of vection-compatible visual motion triggers neural processes related to the discrimination of egomotion-compatibility and involves optic flow parsing, vection perception, and spatial reference frame networks. Yet, vection perception does not emerge until several seconds later. Although the onset latency period is argued to reflect the time required for an observer to resolve the visual-vestibular conflict induced by vection-compatible stimulation (Palmisano et al., 2016), the neural processes that occur in this period are rarely examined. Investigating these processes will be essential if we are to understand the neural mechanisms that underlie vection perception and why the subjective experience of vection varies between individuals.

2. *What is the nature of the relationship between N2 component amplitude and perceived vection strength/intensity?*

   Previous studies report a tentative relationship between parieto-occipital N2 component amplitude and perceived vection strength/intensity (Berti et al., 2019; Keshavarz & Berti, 2014; Wei et al., 2019). In this thesis, a moderate correlation ($\rho = -0.31$) was observed between central (cluster) mean amplitude and perceived vection strength in the vection-compatible stimulation condition (Study 2, Chapter 2.2). However, this failed to reach statistical significance after correction for multiple comparisons (uncorrected $p = 0.018$). Since the ERP components in these correlations occur soon after motion onset and several seconds prior to vection onset, they likely reflect the processing of visual motion properties that are important for later vection perception (e.g. coherency). Future research is required to disambiguate this relationship and its meaningfulness.

3. *Is there a relationship between the attenuated ERPs and decreased alpha power observed in response to vection-compatible motion? Do these different aspects of the EEG signal reflect common processes?*

   In this thesis, vection-compatible visual motion was associated with attenuated central ERPs following motion onset and a decrease of centro-parietal alpha power during prolonged motion exposure. In contrast to oscillations, the neurophysiological mechanisms that produce ERPs are not well understood (Cohen, 2014). Although controversial, there is some evidence suggesting the ERP P1 component is at least partially generated by a phase reset of alpha oscillations (Klimesch et al., 2007). Given the potential link between ERP components and alpha oscillations, future research should investigate the possibility that the ERP and alpha power changes observed in response to vection-compatible motion reflect common neural mechanisms related to the processing of self-motion (compatible) information.

4. *What neural generators are involved in vection-related alpha modulations?*

   Regarding alpha oscillations, this thesis observed that: 1) vection-compatible visual motion is associated with general alpha power decreases, 2) vection onset is associated with a transient alpha power decrease, and 3) ongoing vection perception is associated with alpha power increases. Alpha oscillations are generated primarily in the thalamus and cortex by a variety of neural processes (Clayton et al., 2018). Identifying the neural generators involved in the abovementioned alpha power changes (which was attempted, without success, this thesis), will be important for clarifying the functional role(s) of alpha oscillations in vection perception.

5. *Is there a relationship between age-related changes in alpha power and age-related changes in vection perception?*

   Vection perception varies across the lifespan, with older adults typically reporting weaker vection (e.g. Haibach et al., 2009). Similarly, the properties of alpha oscillations vary with age (Klimesch, 1999). Given the association between alpha oscillations and vection perception reported in this thesis, it would be remiss not to investigate the potential relationship between age, alpha oscillations, and vection perception in future studies.

3.4 The relationship between handedness, lateralization of cortical multisensory vestibular processing, and vection perception

Since vection perception involves reciprocal visual-vestibular interaction (Brandt et al., 1998) and cortical multisensory vestibular processing is dominant in the left hemisphere in left- handers and in the right hemisphere in right-handers (Dieterich et al., 2003; Janzen et al., 2008; Kirsch et al., 2018; Schlindwein et al., 2008), this thesis investigated the potential hemispheric lateralization of vection processing in left- versus right-handers. Overall, left- and right-handers exhibited both similarities and differences in vection-related processing. The following sections discuss a) handedness-dependent vection processing, b) the challenges involved in studying left-handers, and c) the open questions that should be addressed in future research.

a) Handedness-dependent vection processing

This thesis provides initial evidence that vection-related processing differs between left- and right-handers, despite both groups experiencing similar vection perception. The following paragraphs discuss this finding in more detail, focusing on i) handedness differences in pre-vection processing, ii) the relationship between handedness, alpha oscillations, and vection perception, and ii) the functional (in)significance of handedness-dependent vection processing.

Handedness differences in pre-vection processing

This thesis found 1) a larger amplitude difference between vection-compatible and vection-incompatible motion onset evoked ERPs in left-handers and 2) in the same time window, differences in area CSv between left- and right-handers. The CSv area not only prefers egomotion-compatible visual stimulation, but shows suppressed or absent responses during egomotion-incompatible stimulation (Cardin & Smith, 2010; Pitzalis et al., 2013, 2020; Wada et al., 2016; Wall & Smith, 2008). As such, it is possible that the larger ERP difference exhibited by left-handers reflects a greater suppression of CSv activity in response to vection-incompatible (i.e., egomotion-incompatible) versus vection-compatible (i.e., egomotion-compatible) motion, as compared to that observed in right-handers. Importantly, left- and right-handers reported comparable perception during both motion types, indicating that the observed group differences in EEG activity cannot be attributed to one group experiencing more/less egomotion-compatibility during vection-compatible and/or vection-incompatible stimulation, as compared to the other group.

The CSv area is also responsive to vestibular stimulation (Ertl et al., 2017; Smith et al., 2012), making it a candidate location for the integration of visual and vestibular information related to self-motion (Smith, 2021; Smith et al., 2012). Moreover, area CSv receives afferent input from the vestibular system (Smith et al., 2012) and has structural and functional connections with both the ipsi- and contra-lateral posterior insular cortex (PIC) (Smith et al., 2018). Evidence now suggests that the posterior insular cortex comprises two distinct regions: the PIVC, which responds to vestibular input and is suppressed by visual motion stimulation, and the posteriorly adjacent multisensory PIC, which is responsive to both visual and vestibular inputs (Frank et al., 2014, 2016). Due to the limited spatial resolution of EEG source localization techniques, this thesis does not attempt to distinguish between these two areas and instead refers to the general area as the posterior insular/PIVC region. In the same period when left- and right-handers exhibited activity differences in the CSv area, comparison of estimated source activity during vection-compatible versus vection-incompatible motion revealed posterior insula/PIVC differences that were bilateral in left-handers and asymmetrical towards the right hemisphere in right-handers. Based on the outlined connectivity between these regions, this thesis speculates that the handedness-dependent activity patterns in the posterior insular/PIVC region during vection-compatible versus vection-incompatible motion stimulation results in differential afferent (and/or feedback) signals with area CSv, thus producing the observed group differences in EEG activity. Although further research is needed to determine the validity of this speculation, the findings of this thesis indicate that pre-vection processing is modulated by handedness.

The relationship between handedness, alpha oscillations, and vection perception

This thesis found that although left- and right-handers exhibit a centro-parietal alpha power decrease during vection-inducing visual motion stimulation, this alpha power decrease has a left lateralized topography in left-handers and a bilateral midline topography in right-handers. Subsequent time-frequency analyses revealed that despite these topographical differences, left- and right-handers exhibit a similar pattern of alpha band changes over the course of vection perception (i.e., a transient alpha power decrease around vection onset and increasing alpha power during ongoing vection perception). Further research is required to determine the neural generators involved in the abovementioned alpha band modulations and to disclose how those generators might differ in such a way as to give rise to the different topographies exhibited by left- and right-handers. Altogether, left- and right-handers showed similar vection-specific alpha power changes but at different topographical locations, supporting the idea that handedness influences vection processing without altering vection perception. Differences in vection processing between left- and right-handers are likely a consequence of both groups processing cortical multisensory vestibular information in a lateralized manner, which in turn affects the visual-vestibular interaction underlying vection perception.

The functional (in)significance of handedness-dependent vection processing

This thesis found that despite exhibiting vection-related differences in EEG activity, left- and right-handers experienced comparable vection perception. This conflicts with previous work showing quicker perceptual transitions from world- to self-motion (i.e., vection onset latency) in right-handers, compared to left-handers (Arshad et al., 2019). One possible explanation for these incongruent findings is that left- and right-handers differ in their perception of circular vection, which was induced in the previous work (Arshad et al., 2019), but not in their perception of roll vection, which was induced in this thesis. Alternatively, the vection generated in the present thesis may have been more compelling and therefore less variable among individuals and groups, as compared to the vection generated in the study by Arshad et al. (2019). Support from this interpretation comes from two observations: 1) in contrast to those reported in Arshad et al. (2019), the present thesis observed substantially shorter onset latencies, which suggests a more intense vection experience, and 2) in the study by Arshad et al. (2019), reported onset latencies appear to be much more variable among left-handers than right-handers. Taken together with the limited sample size (N = 10 per group), these factors make it difficult to discern whether the perceptual differences reported by Arshad et al. (2019) are true handedness differences or whether they are a consequence of weak, unstable vection that happened to be more variable amongst individuals in the left-hander group. Further research is necessary to resolve this issue and to clarify the relationship between handedness and vection perception in various planes/axes. Nevertheless, this thesis found that left- and right-handers exhibit differences in vection-related processing but not in vection perception, indicating that the observed differences in vection-related processing are functionally insignificant, at least in this experimental context.

b) The challenges involved in studying left-handers

Over the course of thesis, several challenges emerged regarding the investigation of vection in left-handed individuals. Although handedness seems like a straightforward trait, there is no universally accepted method of measuring it (Papadatou-Pastou et al., 2020) and even the most commonly employed method - the Edinburgh Handedness Inventory (EHI; Oldfield, 1971) – is not without controversy (see Edlin et al., 2015 for further discussion). The development of preferred handedness is affected by several factors, including familial and cultural preferences, educational practices, the prevalence of devices that are more suitable for one hand over the other, and genetic factors (Hardyck & Petrinovich, 1977). Moreover, several of these factors are/have in the past been biased against a left-hand preference (Hardyck & Petrinovich, 1977). For example, many everyday items are made by default for right-handers (e.g. scissors), which forces left-handers to learn to perform some motor tasks in a right-handed manner. In turn, this leads to left-handers exhibiting a weaker handedness preference, at least according to many handedness assessment methods, compared to right-handers. Indeed, during data collection for this thesis, several individuals who self-reported as strictly left-handed were classified by the EHI as having mixed-handedness (note: the data from these individuals is not included in this thesis). Furthermore, in the two studies included in this thesis, the left-hander group exhibited more variable handedness laterality quotients (i.e., handedness scores) than the right-hander group. As is argued in Study 2 (Chapter 2.2), this weaker, more variable left-handedness preference may have influenced some of the findings in this thesis.

A further challenge relates to the fact that left-handers make up only about 10% of the population (Papadatou-Pastou et al., 2020) and are a largely understudied group. For instance, left-handers are commonly excluded from neuroscientific and psychological research on the assumption that their inclusion would reduce sample homogeneity and potentially interfere with results. This is largely based on evidence indicating an association between handedness and differences in brain morphology (e.g., Amunts et al., 2000; Budisavljevic et al., 2021; Seizeur et al., 2014), as well as cerebral anatomical and functional lateralization (e.g., Cuzzocreo et al., 2009; Johnstone et al., 2021; Tremblay et al., 2004). On a practical level, even when a study does include left-handers as a group of interest, their relatively low prevalence means it is often difficult to recruit such individuals to participate in research.

c) Handedness and vection perception: open questions

The findings of this thesis raise several new questions about the relationship between handedness and vection processing. Several of these questions are briefly outlined below.

1. *Is there a relationship between handedness-dependent activity in the posterior insula/PIVC and handedness differences in response to vection-(in)compatible visual motion in the CSv area?*
   This thesis (Study 2, Chapter 2.2) speculates that handedness-dependent activity patterns in the posterior insular/PIVC region during vection-compatible versus vection-incompatible visual motion results in differential afferent and/or feedback signals with area CSv, thus producing differences in EEG activity between left- right-handers. Future studies are required to determine the validity of this speculation, perhaps employing a) structural MRI to examine potential structural/localization differences of the CSv area between left- and right-handers, and b) EEG/MRI connectivity methods to examine the connectivity between the posterior insula/PIVC and the CSv area in left- versus right-handers.

2. *Do left- and right-handers differ in their discrimination of (visual) egomotion-compatibility?*
   This thesis reports that left- and right-handers exhibit activity differences in the CSv area, in response to vection-compatible versus vection-incompatible visual motion. As the CSv area is known to discriminate between egomotion-compatible and egomotion-incompatible visual stimulation (e.g., Pitzalis et al., 2020; Smith, 2021), a question arises about whether left- and

right-handers differ in their perceptual discrimination of visual egomotion-compatibility. This possibility should be investigated in future research, using visual motion stimuli that vary in their egomotion-compatibility (e.g. stimuli with differing amounts of coherency).

3. *Is there a relationship between handedness and the consequences of vection perception?*
   In this thesis, left- and right-handers experienced comparable vection perception, despite differences in vection-related processing. However, the presence of vection may itself alter behaviour and cognition (see Chapter 1.1 for discussion). To definitively determine the functional significance of handedness differences in vection-related processing, future research will need to investigate if these differences alter the behavioural and cognitive consequences of vection perception.

4. *What does vection perception/processing look like in individuals who are ambidextrous/have mixed handedness?*
   An inevitable follow-up to this thesis would be to ask how vection perception and processing functions in ambidextrous/mixed-handedness individuals. Such research will require careful design, as some evidence indicates that the lateralization of cerebral functions is organized along a continuum of handedness (Hardyck & Petrinovich, 1977). Previous imaging studies have demonstrated that vestibular processing is regularly distributed, with a dominance of the right hemisphere in right-handers and of the left hemisphere in left-handers (Dieterich et al., 2003; Kirsch et al., 2018), however, these studies were not focused on ambidextrous individuals. Further, it is not always the case that cerebral organization in right-handers is simply mirrored in left-handers (Hardyck & Petrinovich, 1977) and that ambidextrous/mixed-handedness individuals will fall somewhere in between. Altogether, it may be prudent for future research to investigate vection perception along a continuum of handedness, instead of comparing 'categories' of handedness (i.e., left- versus right- versus mixed-handedness).

3.5 Future directions in vection research

Over the course of this thesis, several limitations and future directions in vection research have become apparent. These are briefly discussed below.

Vection perception under naturalistic conditions

There is a growing acceptance in the neuroscientific community that more naturalistic experiments are required if we are to understand how both behaviour and the brain operate in natural contexts. In vection research, this will require us to move away from two highly artificial and almost ubiquitous trends in vection studies: 1) the use of simplistic, unnatural visual motion stimuli and 2) the treatment of all eye movements as confounding factors that should be eliminated. With regard to the former, most vection studies (including those in this thesis) employ simplistic visual motion stimuli such as dot clouds or stripe patterns. Moreover, most stimuli present coherent global motion (i.e., no local motion disturbances) along a single plane or axis. Although such stimuli facilitate the development of appropriate control stimuli (i.e., it is much easier to develop a control stimulus for a dot cloud than for a realistic visual motion scene) and are capable of inducing vection perception, they lack many features of natural optic flow and real visual scenes. This limitation should be addressed in future research, perhaps using movies (see e.g. Pitzalis et al., 2020) or virtual reality environments. Indeed, the realism of even simplistic stimuli like dot clouds could be improved by the addition of dynamic motion (e.g., (de)accelerations, changes in the plane/axis of motion).

With regard to the latter trend, most vection studies aim to eliminate or, at the very least, attenuate eye movements. Although reasonable in some contexts (e.g. attenuating eye blinks and movements to reduce artefacts in neuroimaging signals), this approach ignores the fact that many vection-compatible stimuli actually trigger eye movements (e.g. continuous roll motion typically triggers torsional nystagmus). Further, it ignores reality because most natural behaviours are accompanied by eye movements (Lappe et al., 1999). Indeed, during actual self-motion eye movements are essential for maintaining stable vision and directing gaze to objects of interest (Lappe et al., 1999). The few studies that have investigated the relationship between eye movements and vection perception have produced mixed evidence. For instance, it has been reported that the direction of horizontal circular vection is independent of the direction of eye movements induced by motion stimulation of the central visual field (Brandt et al., 1973). In contrast, compensatory eye movements have been linked to increases in vection strength (Kim & Palmisano, 2010), and optokinetic nystagmus has been found to correlate positively with self-motion perception (Thilo et al., 2002). Yet, most vection studies do not consider eye movements beyond requiring participants to fixate so that vection might be facilitated (see e.g., Fushiki et al., 2000; Howard & Howard, 1994; Tarita-Nistor et al., 2006) and signal artefacts may be reduced. Altogether, the reliance on artificial stimuli and the reluctance to directly investigate the intersection of eye movements and vection perception means that vection research may be failing to capture important aspects of how vection perception operates in the real world.

The relationship between vection perception, the sensorimotor network, and the control of self-motion

It is commonly acknowledged that somatosensory information contributes to self-motion perception (see e.g. Brandt, 2003). Yet, relatively little is known about the contribution of somatosensory information and its integration with visual and vestibular information in vection perception. It is argued that the biological function of perception is the control of action for adaptive behaviour (Warren, 1995). Accordingly, the function of vection/self-motion perception would be to facilitate the adaptive control of self-motion. It is therefore unsurprising that several neuroimaging studies have reported vection-related activity within somatosensory areas and the wider sensorimotor network (see Table 2, Chapter 1.4). Given the findings of this thesis and the recent suggestion that the CSv area acts as an interface between sensory and motor systems for the control of locomotion (Smith, 2021), future research should not only investigate whether vection-related activity in this region is associated with self-motion control but should also explore if such an association is modulated by handedness. As EEG may be easily combined with posturography and motion tracking systems, it would provide an ideal method for future investigations into the relationship between vection perception, the sensorimotor network, and the control of self-motion.

Susceptibility and resistance to vection perception

Although there is some evidence that vection-susceptibility is affected by individual factors (e.g., personality traits and age), it is largely unclear why some individuals feel compelling vection while others experience weak, infrequent vection or even a total absence of vection. Indeed, vection studies commonly exclude individuals who do not perceive (sufficient) vection (e.g. Kirollos et al., 2017). Consequently, almost nothing is known about the differences between vection-susceptible and vection-resistant individuals, including for example, whether (and how) the neural processes evoked by vection-compatible motion differ between such individuals. Future investigation of vection-susceptible versus vection-resistant individuals, and their respective neural processing of vection-comaptible motion, would likley provide important insights into vection perception and its underlying neural mechansisms.

Vection perception in healthy older adults and clinical populations

Healthy older adults exposed to vection-compatible stimulation exhibit decreased vection perception and increased actual motion (Haibach et al., 2009). It is thought that age-related sensory deficits alter the multisensory interactions responsible for vection perception, which results in a dissociation between actual and perceived self-motion that, in turn, increases fall risk (Haibach et al., 2009). This raises questions about how various sensory impairments might alter the multisensory interactions involved in vection perception and self-motion control. Although vection perception relies heavily upon visual-vestibular interaction, there is evidence indicating that a functional peripheral vestibular system is not required for vection perception (Zee et al., 1976). Further, vection perception is also possible with mild peripheral visual field loss (Tarita-Nistor et al., 2014) or central visual field loss (Fushiki et al., 1999). Observations that visual and vestibular sensory deficits do not prohibit the perception of vection points to a degree of adaptability (and/or redundancy) in the multisensory interactions involved in vection perception. By investigating vection perception and self-motion control in healthy older adults and individuals with clinical sensory deficits, future research may be able to not only enhance our understanding of vection perception but to use the resulting knowledge to develop methods of improving self-motion perception and control in these populations.

3.6 A brief note on the functional significance of vection

The functional significance of vection remains a sometimes controversial and incompletely studied topic (for review see Palmisano et al., 2015; Pitzalis et al., 2020; Riecke, 2015). In particular, the behavioural relevance of consciously experiencing vection/our own self-motion is a source of much debate. On one hand, it is argued that vection is an epiphenomenal by-product of self-motion control, emerging too slowly to be useful for self-motion control (see Palmisano et al., 2015 for discussion; Warren, 1995). Relatedly, the popular conceptualisation of vection as an ‘illusion’ of self-motion, infers that vection is an unusual perceptual error (for review: Palmisano et al., 2015). On the other hand, there is increasing evidence that vection plays a role in our ability to make judgements about our self-motion, to control our self-motion, and to facilitate our spatial orientation and navigation in both real and virtual environments (for review: Palmisano et al., 2015; Riecke et al., 2015). Further, limitations of the vestibular system may necessitate an ability to perceive (visually-induced) vection and control self-motion at constant velocities (Brandt, 2003; Dichgans & Brandt, 1978). Together, this suggests that vection is involved in updating internal representations of the self in relation to the environment, pointing to potential functional significance.

3.7 Conclusion

By employing EEG techniques to study vection perception and examining the potential hemispheric lateralization of vection processing in left- and right-handers, this thesis enhanced our knowledge of vection perception and its underlying neural mechanisms. The findings of this thesis emphasise the benefits of EEG recordings and their remarkable temporal accuracy in vection research, disclosing the temporal activation of the vection network by vection-compatible stimulation and identifying vection-specific alpha oscillation modulations. Furthermore, this thesis showed that left- and right-handers exhibit both similarities and differences in vection processing and perception. In particular, it was revealed that handedness influences aspects of vection processing but not vection perception. Altogether, the findings from this thesis have important implications for future research as they highlight the importance of temporal accuracy and the relevance of handedness in the study of vection perception and its underlying neural mechanisms.

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LIST OF PUBLICATIONS

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EIDESSTATTLICHE VERSICHERUNG / AFFIDAVIT

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation **„EEG analysis of visually-induced vection in left- and right-handers“** selbstständig angefertigt habe, 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.

I hereby confirm that the dissertation **„EEG analysis of visually-induced vection in left- and right-handers“** is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

Michaela McAssey

München, den 31.05.2022
Munich 31.05.2022

DECLARATION OF AUTHOR CONTRIBUTIONS

Study 1: Different EEG brain activity in right and left handers during visually-induced self-motion perception

Authors: Michaela McAssey, James Dowsett, Valerie Kirsch, Thomas Brandt, Marianne Dieterich

Michaela McAssey, Marianne Dieterich, and Thomas Brandt conceived the experiment. Michaela McAssey and James Dowsett programmed the experiment. Michaela McAssey collected the data. Michaela McAssey analysed the data with the assistance of James Dowsett and Valerie Kirsch. Michaela McAssey drafted the manuscript, with feedback and revisions from Marianne Dieterich and Thomas Brandt. All authors commented on and approved the final manuscript. Michaela McAssey is the only first author of the paper.

Study 2: EEG analysis of the visual motion activated vection network in left- and right-handers

Authors: Michaela McAssey, Thomas Brandt, Marianne Dieterich

Michaela McAssey, Marianne Dieterich, and Thomas Brandt conceived the experiment. Michaela McAssey collected the data. Michaela McAssey analysed the data. Michaela McAssey drafted the manuscript, with feedback and revisions from Marianne Dieterich and Thomas Brandt. All authors commented on and approved the final manuscript. Michaela McAssey is the only first author of the paper.

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