Standing Well

Lubeck, A.J.A.

2016

Chapter 1

Introduction

1.1. Introduction

Our senses are intriguing structures that enable us to perceive the world and to control our actions. While navigating through the world we integrate signals coming from our senses into one stable percept. Most of the time these signals are in agreement with each other. As we are walking or riding our bike we see the environment moving past ourselves, our somatosensory system senses the air flow, and we perceive our linear and angular acceleration with the organs of balance. However, we can put ourselves in situations in which the information from these senses is conflicting. In fact, if we do that, we do this most of the time just for fun!

In many of these situations there is a mismatch between information originating from the eyes and from the organs of balance, also called a visual-vestibular conflict. This conflict can be caused by bodily motion that is not accompanied by congruent visual motion, for example when reading a book in a moving car. We sense the physical motion of the car and ourselves with the organs of balance, but we see a stationary book and the stationary inside of the car. As another example, a visual-vestibular conflict can also be evoked by seeing motion in the absence of any bodily motion. Examples of this type of conflict are watching a movie at the cinema, watching television, or playing a game on your computer. In these situations the visual cues are suggestive of bodily self-motion while the organs of balance do not register (congruent) bodily motion; instead, the organs of balance sense that we are standing or sitting still. In this thesis I will focus on visual-vestibular conflicts caused by the latter: seeing motion in the absence of physical motion.

A visual-vestibular conflict can cause a broad range of motor- and perceptual effects that, in certain cases, may have a serious impact on well-being and behaviour of the observer. Although we know that such conflicting sensory cues cause changes in motor and perceptual responses, we do not sufficiently understand the central nervous system (CNS) processes at work during a visual-vestibular conflict. With this thesis I therefore aim to contribute to a better understanding of this process. Here it is hypothesized that the CNS uses a mechanism that incorporates an internal model (outlined below) that drives, or at least partly modulates, specific motor- and perceptual responses. By monitoring the patterns of these responses we can get insight into the CNS processes at work during a visual-vestibular conflict. To this end, we use in a series of experiments various visual manipulations (e.g. stereoscopic 3D) to modulate the visual-vestibular conflict, allowing us to examine the dynamics of the CNS processes. Before I elaborate on the motor and perceptual responses examined, I will introduce the theoretical framework on which the experiments in this thesis are based. I will end this chapter with an overview of the research questions that are addressed in the next chapters.

1.2. How do you expect the vertical to be oriented?

The CNS can be considered a "black box" that is activated by input, in this thesis sensory stimuli, and produces output, i.e. motor and perceptual responses (Fig. 1.1). In this thesis two sensory inputs are of importance: visual motion cues and vestibular cues. As will become clear in the next sections, especially cues that contain information about Earth-verticality are of importance in this thesis.

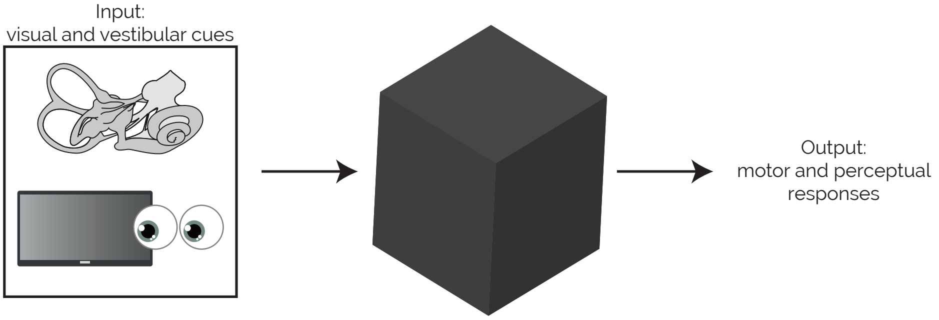

Figure 1.1. A schematic illustration of the general experimental design used in this thesis to study the central nervous system (CNS) workings, here depicted as a black box, during a visual-vestibular conflict. A visual-vestibular conflict can be evoked by providing visual cues that differ from the cues provided by the organs of balance. This visual-vestibular conflict is proposed to exert an influence on motor and perceptual responses. By monitoring these responses, we can obtain more insight into the CNS processes at issue.

Although humans are most of the time not consciously aware of which way is "up" and "down", that is, what is Earth-vertical, many of our activities are coordinated with respect to the Earth-vertical, such as standing, walking, cycling, or even just sitting upright. A simple servo-system (see e.g. Bos[1]) based on a negative feedback loop, will not suffice to control these complex behaviours, because of several reasons[1–4]. First, our senses are not perfect and can exhibit variations due to, for example pathology or ageing. Second, neural delays cause sensory information, such as visual information[5], to be available too late for adequate regulation by such a negative feedback mechanism[6]. And third, inertial accelerations due to bodily motion are physically indistinguishable from accelerations due to gravity, known as the equivalence principle of Einstein[7]. In other words, Einstein stated that there are no accelerometers capable of making the distinction between inertial and gravitational (or free fall) accelerations, which thus also holds for the organs of balance. Yet, on Earth, clearly we do not perceive constant upward motion with an acceleration of 9.8 m/s^2, indicating that our CNS is capable of distinguishing between inertial and gravitational accelerations. Thus the question is what enables us to distinguish between these two types of acceleration. One important distinction between inertial and gravitational acceleration is the notion that inertial accelerations associated with self-motion are generally variable, while gravity on Earth is always constant, at least in an Earth-fixed frame of reference. One concept that takes this notion into account and that could facilitate the CNS to optimise the estimation of self-motion and orientation with respect to gravity, is a so-called internal model. Internal models represent general neural processes that mimic the behaviour of natural processes by combining afferent (e.g. sensory cues) and efferent information (e.g. efference copies)[6,8,9]. Several studies have found evidence in favour of an internal model, that contains an estimate of the orientation of gravity, being a mechanism applied by the CNS to also resolve the ambiguity between inertial and gravitational accelerations[6,8,10]. Next to the distinction between these two types of acceleration, internal models that estimate verticality have been proposed to play a significant role in a number of other motor and perceptual responses, such as motion sickness[1,2] and postural control[2,3,11–13].

1.3. An internal model of verticality to deal with a visual-vestibular conflict

In order to orient ourselves upright with respect to the Earth-vertical, i.e. the orientation of gravity, a correct perception of verticality has shown to be critical[2,3,11–13]. In line with the literature, in this thesis it is proposed that the CNS employs an internal model to construct a perception of verticality to control postural orientation, here coined an internal model of verticality. This internal model incorporates visual, vestibular and somatosensory input to construct a neural representation of verticality. Because the internal model incorporates visual and vestibular cues, it is proposed to be part of the CNS workings during a visual-vestibular conflict.

One theory that incorporates an internal model of verticality in the control of postural orientation, is the motion sickness theory (MST)[1,2]. This theory proposes that a visual-vestibular conflict induces a mismatch between the actual postural orientation and the postural orientation expected by the internal model over verticality, resulting in postural adjustments in order to reduce this mismatch. Moreover, a mismatch between what is expected and what is actually sensed, is proposed to be the underlying cause motion sickness. Before addressing these responses, I will further introduce the MST.

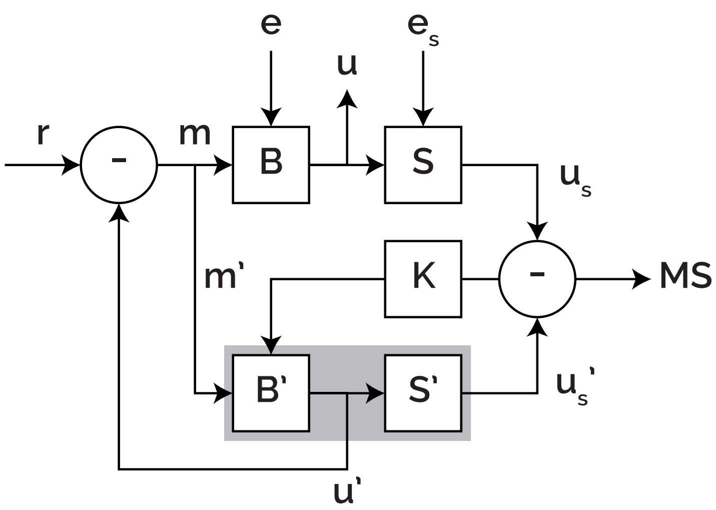

Figure 1.2. Simplified model of the motion sickness theory (MST). The components within the grey area constitute the internal model of verticality. See text below for an explanation of all the components.

The MST is an elaboration of the so-called sensory conflict theory as postulated by Oman[14], and incorporates an internal model of sensory and bodily states, such as an estimate of postural orientation (Fig. 1.2, grey area). To fully explain the workings of the MST during a visual-vestibular conflict, it is important to distinguish between the sensed vertical, expected vertical and the expected sensed vertical. First, the desired body posture, represented by **r**, is in this thesis an upright posture parallel to the orientation of gravity. To achieve this desired posture, motor commands (**m**) are sent to the muscles in the body (**B**), and an efference copy (**m'**) is sent to the neural representation of the body (**B'**). Physical perturbations (**e**), e.g. a push or a gust of wind, act upon the body and destabilize the standing posture. Sensory perturbations ($\mathbf{e}_s$), such as visual motion or galvanic stimulation, act upon the sensory modalities (**S**). **S** thus comprises the visual, vestibular and proprioceptive sensors, while **S'** refers to the neural representation of these sensors. The actual orientation of the longitudinal body axis is represented by **u**, and **u'** is the neural estimate thereof; the latter is here called the expected vertical. Note that **u'** is calculated on the basis of efference copies and sensory signals (through comparison with $\mathbf{u}_s'$). The difference between **u** and **u'** is proposed to be involved in the regulation of postural orientation. The sensed postural orientation is annotated with $\mathbf{u}_s$, and $\mathbf{u}_s'$ represents its neural representation thereof, here further coined the sensed vertical and expected sensed vertical respectively. A mismatch between $\mathbf{u}_s$ and $\mathbf{u}_s'$ is proposed to lead to motion sickness (**MS**), including visually induced motion sickness (VIMS). When standing upright, both the expected vertical (**u'**) and expected sensed vertical ($\mathbf{u}_s'$) are under normal circumstances, i.e. when there are no conflicting sensory cues, oriented parallel to the body axis ($\mathbf{u}$), the sensed vertical ($\mathbf{u_s}$), and the Earth-vertical (Fig 1.3; row 1). In other words, there is no conflict between what is expected ($\mathbf{u'}$ and $\mathbf{u_s'}$) and the actual orientation ($\mathbf{u}$) and sensed orientation ($\mathbf{u_s}$).

Now consider the situation in which we stand quietly in an otherwise darkened room, and view clockwise roll-motion around the line of sight. The clockwise roll-motion is considered a sensory perturbation ($\mathbf{e_s}$) that provides visual cues indicating self-motion in a counter clockwise direction [1], while the vestibular (and somatosensory) cues suggest no self-rotation. Due to the conflicting sensory cues the sensed vertical ($\mathbf{u_s}$) first tilts into the rotation direction, followed by a tilt of the body axis ($\mathbf{u}$) into the rotation direction, i.e. in the clockwise direction (Fig. 1.3; 2nd row). Due to the tilts of $\mathbf{u}$ and $\mathbf{u_s}$, a mismatch arises with their respective neural representations, $\mathbf{u'}$ and $\mathbf{u_s'}$, further referred to as an internal mismatch. The internal mismatch between the orientation of the body axis ($\mathbf{u}$) and the expectation thereof ($\mathbf{u'}$) is proposed to result in a postural deviation towards the rotation direction. Also, VIMS symptoms are thought to occur, reflecting the mismatch between the sensed vertical ($\mathbf{u_s}$) and the expected sensed vertical ($\mathbf{u_s'}$).

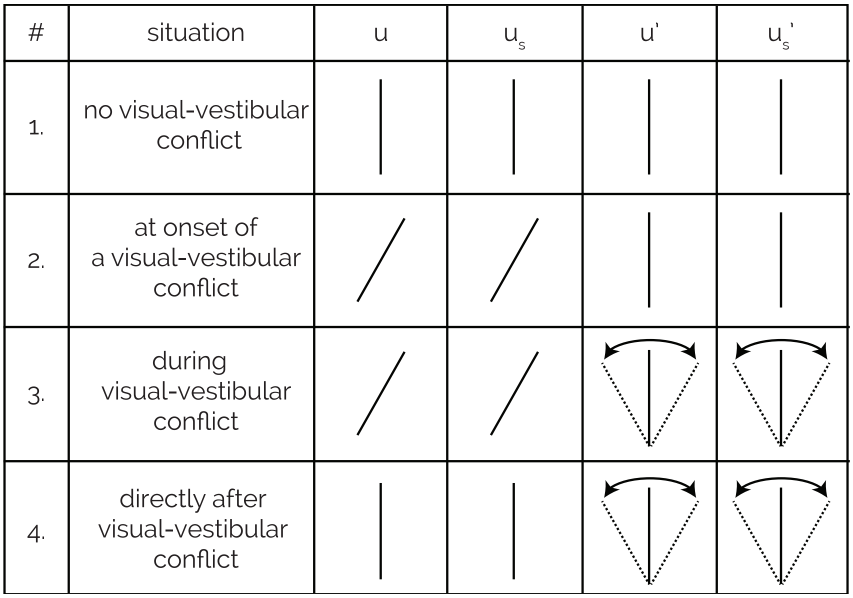

Figure 1.3. Schematic representation of proposed effects of clockwise visual roll-motion on the average orientation of the body axis (u), the sensed vertical (us), the expected vertical (u') and the expected sensed vertical (us'). See text for full explanation.

When the visual-vestibular conflict persists, the internal model tries to adapt in order to minimize the internal mismatches (Fig 1.3; row 3 and row 4). However, as long as the internal model does not succeed in minimizing

1 Under normal circumstances, when our body and head are rotated in the counter clockwise direction (ignoring hereby ocular torsion), we see the environment rotating in a clockwise direction with reference to our own body.

the mismatches, postural deviations away from the true vertical, and VIMS persist. These changes in the internal model are visible whilst a visual-vestibular conflict (Fig. 1.3; 3rd row), and (for a certain period) after the visual-vestibular conflict (Fig. 1.3; 4th row). To study the exogenous (i.e. the direct influence of sensory perturbations as illustrated in the 2nd and 3rd row of Fig. 1.3) and endogenous (i.e. influence of internal mis conflict on the CNS workings, we have obtained measurements on postural orientation during occurrences of a visual-vestibular conflict and directly after cessation of the visual-vestibular conflict. This topic will be further addressed in the next section.

Finally, with this theoretical framework we are also able to substantiate how certain visual manipulations will influence the visual-vestibular conflict and the motor and perceptual responses, enabling us to further unravel the CNS workings. At the end of this chapter I will introduce the visual manipulations we used and how we expected them to influence the visual-vestibular conflict and respective motor and perceptual responses.

Besides roll-motion around the line of sight, motion pictures containing ample linear and angular motion in all dimensions, such as movies and computer games, can also induce motor- and perceptual responses[15–21]. Motion pictures best resemble the stimuli that we are exposed to in daily life, and already have been used by many other researchers to study the influence of the visual-vestibular conflict on motor- and perceptual responses (e.g.[15–21]). These motion pictures often contain roll- and tilt- motion indicating a tilt of what is Earth-vertical, thereby causing internal mismatches between $\mathbf{u}$ and $\mathbf{u}_s$ and their respective neural representations ($\mathbf{u}'$ and $\mathbf{u}_s'$) leading to postural deviations and VIMS.

1.4. Motor and perceptual responses

1.4.1. Postural control

Postural control has been defined as "the act of maintaining, achieving or restoring a state of balance during any posture or activity"[22]. In this thesis the focus lies on how we maintain a standing upright posture. It is generally recognized that the goal of postural control is to keep the centre of mass above the base of support[23,24].

One frequently used method to obtain insight into how a standing posture is maintained, is by measuring the centre of pressure (CoP) with a force platform. The CoP is the point of application of the resultant ground reaction force vector (Fig. 1.4), and, is highly correlated with movements of the centre of mass, at least, during quiet upright stance[24]. The ground reaction force vector represents the weighted average of pressures distributed over the area under the feet that is in contact with the support surface[24]. When standing with both feet on the ground, the position of the

CoP is located somewhere in the base of support[24,25]. Even if one tries to stand still, the CoP always moves around in what may appear to be an erratic fashion. However, these CoP excursions are suggested to be a structured output containing valuable information about how the CNS controls body posture[26,27]. We propose that several characteristics of these CoP displacements (partly) reflect the difference between the expected vertical (**u'**) and the orientation of the longitudinal body axis (**u**).

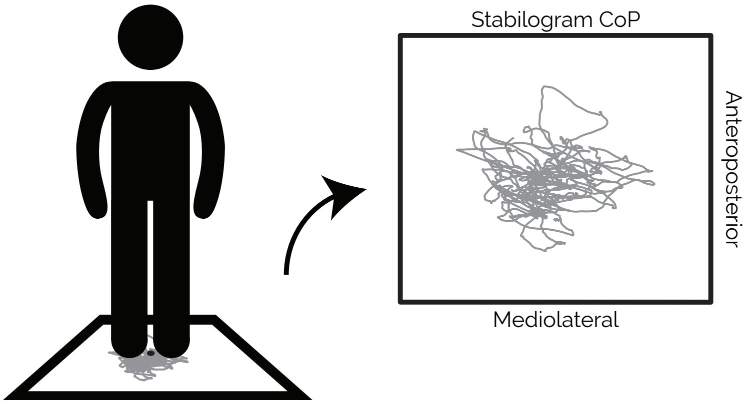

Figure 1.4. Schematic presentation of a centre of pressure (CoP) measurement on a force platform (left). The CoP (black dot) is in the case of quiet stance located somewhere in the base of support and moves constantly (grey line). The stabilogram (right) depicts an example of the movement of the CoP in fore-after (anteroposterior) and left-right (mediolateral) directions.

Several characteristics of postural sway have shown to be affected during viewing motion pictures. More specifically, participants sway significantly more and further whilst viewing motion pictures compared to before viewing[16,19,21,28,29]. Less is known about how postural sway is affected by certain visual manipulations, such as stereoscopic 3D. As explained earlier, the increase in postural sway during exposure to roll-motion around the line of sight is also direction specific; that is, the CoP deviates into the direction of rotation during exposure to roll-motion around the line of sight[30–32].

Apart from these exogenous – direct – effects of a visual-vestibular conflict on postural sway, postural sway can also be affected in an indirect or endogenous way by a visual-vestibular conflict through changes in the internal model of verticality. By measuring postural sway with eyes closed, the direct, exogenous influence of visual stimuli on postural sway could be excluded. When postural sway is obtained with closed eyes after viewing motion stimuli, it is typically increased in magnitude, compared to before watching[33–35]. As explained in Fig. 1.3, this increase in postural sway is thought to reflect the mismatch between u and u' that exists directly after the cessation of a visual-vestibular conflict.

1.4.2. The subjective visual vertical

The deviation of what we perceive as vertical with respect to the Earth-vertical is often quantified using a perceptual task. A method often used to measure deviations of perceived verticality involves aligning a visible rod – the so-called subjective visual vertical (SVV) – to the perceived vertical. Just as for postural control, the expected vertical (**u'**) is proposed to play a central role in the orientation of the SVV. Generally, the SVV is included as a dependent variable when visual roll-motion around the line of sight is used to induce a visual-vestibular conflict. Just as postural sway, experimental evidence shows that the SVV deviates into the direction of rotation during exposure to roll-motion around the line of sight[30–32].

Although postural control and the SVV are proposed to be controlled by the same working mechanism, and exhibit similar effects due to exposure to roll-motion, they do not have to change in similar ways during a visual-vestibular conflict. Several other factors during a visual-vestibular conflict may affect the SVV differently than postural sway. Vestibular stimulation such as galvanic vestibular stimulation, for example, has shown to be able to differently affect postural sway and the SVV[36]. Moreover, the SVV orientation and the estimate of postural orientation have shown to be dissociated in patients after stroke[11,37,38], suggesting that other CNS processes, in addition to an internal model of verticality, can differentially influence these outcome measures. Despite these differences, we yet assume that in healthy participants postural sway and the SVV are similarly controlled by the expected vertical (**u'**) and deviation thereof, thus reflecting the internal mismatch between **u** and **u'**.

1.4.3. Visually induced motion sickness (VIMS)

According to the MST, visually induced motion sickness (VIMS) symptoms arise when an internal mismatch exists between the sensed vertical ($\mathbf{u}_s$) and the expected sensed vertical ($\mathbf{u}_s'$)[2,39,40]. VIMS is a condition in which one experiences symptoms similar to motion sickness due to viewing motion while being physically stationary[15,41–43]. Typical VIMS symptoms include drowsiness, pallor, cold sweat, oculomotor disturbances, disorientation and nausea (see e.g. [44,45]), symptoms equal to those associated with motion sickness in general. A large body of literature underscores that virtually all devices that display motion are capable of inducing VIMS, see e.g.[20,28,46–51]. Although all these devices can trigger VIMS, I chose to use devices that most of us are exposed to on a regular basis: televisions and projection screens.

It is well established that 2D motion stimuli can cause VIMS while actively gaming and while just passive viewing[20,21,28,35,49,52–54]. Also, 3D motion pictures are capable of causing VIMS and have been found to lead to more severe VIMS symptoms than viewing 2D motion pictures[15,17,55–57]. As described earlier, it is proposed that roll-motion around the line of sight is also able to cause a deviation of the expected sensed vertical (**u_s'**), introducing an internal mismatch that results in VIMS. Research has already shown that participants can experience VIMS symptoms during exposure to visual pattern rotation around the line of sight[58,59].

1.4.4. A note on vection

One other response that is closely related to postural sway[60] and VIMS[61,62] is vection, a feeling of self-motion while being physically stationary[63]. Vection can be caused by seeing large visual-field motion stimuli[63]. It thus may seem rather straightforward to include vection as a primary response in the experiments. However, because of several reasons, we decided not to include vection as a primary response. One important reason is that the focus of this thesis is to examine the influence of a visual-vestibular conflict on postural sway and VIMS. In **Chapter 8** vection and the reasons why it was not included as a primary response are further discussed.

1.5. What if the subjective vertical is wrong?

Up till now I considered consequences of an internal mismatch evoked by an external sensory perturbation (**e_s**), in the form of visual motion. But what if the expected vertical (**u'**) and expected sensed vertical (**u_s'**) chronically deviate from the Earth-vertical due to a maladapted internal model of verticality? Such a maladapted internal model of verticality can be result of a vestibular deficit or (unilateral) vestibular loss. After the initial deficit or loss, in most patients the CNS will adapt by compensating for the altered vestibular signals, coined vestibular compensation[64]. For example, visual cues and vestibular cues can be reweighted in response to the changed, vestibular cues[65]. These patients do suffer from vestibular symptoms (e.g. dizziness, nausea, blurred vision, postural instability) during the acute phase, but once the CNS has adapted, symptoms usually disappear[66]. The CNS also correctly readapts in most patients when the inflammation has disappeared, and vestibular function is restored. However, a small group of patients continues to report vestibular symptoms after the inflammation has disappeared[67]. They report aggravation of their symptoms when exposed to challenging visual environments, often containing visual motion[65,68]. We suggest that in this particular group of patients, called visual-vestibular mismatch (VVM) patients, the CNS has not properly adapted the internal model of verticality after the inflammation disappeared, leaving these individuals with a maladapted expected vertical (**u'**) and expected sensed vertical (**u_s'**).

1.6. General aim and outline of the thesis

With this thesis we aim to open our "neural black box", i.e. the central nervous system, by examining its working mechanism during a visual-vestibular conflict. To induce a visual-vestibular conflict we use various manipulations of visual stimuli, whereas the vestibular cues were not manipulated; i.e. participants were instructed to maintain an upright body orientation in all experiments described here.

Although this aim focuses on a theoretical issue, this thesis is also interesting from an applied point of view. For example, research into how visual manipulations influence a visual-vestibular conflict and the respective motor and perceptual responses could aid in the development of motion pictures. Depending on the purpose (e.g. therapeutically or entertainment), the visual-vestibular conflict and ensuing motor and perceptual responses could be enhanced or suppressed by including or excluding certain visual manipulations.

We first asked in **Chapter 2** whether the presence of visual motion in visual stimuli is crucial to induce a visual-vestibular conflict. To date, nearly all studies on the influence of a visual-vestibular conflict tested only the effects of visual motion stimuli on motor and perceptual responses, leaving the question open whether visual motion is necessary to cause a visual-vestibular conflict. In **Chapter 2** we exposed participants to both motion and still images while measuring both postural sway and VIMS. We hypothesized that visual motion would be necessary to cause a visual-vestibular conflict, thereby only resulting in increased postural sway and VIMS when participants were exposed to visual motion as compared to exposure to still images.

Next to visual motion, with improvements in 3D technology, the public health concern that viewing 3D has larger potential for adverse effects, compared to 2D motion pictures, is growing. Hence, in **Chapter 3** we first asked whether viewing a 3D stimulus at the cinema would cause an increase in postural sway and VIMS. To that end, participants were exposed to a 3D movie at the cinema, and postural sway and VIMS were measured directly before and after exposure. However, we could not answer the question whether 3D stimuli would cause a larger visual-vestibular conflict compared to viewing 2D stimuli. Moreover, no other study has yet addressed this question. Therefore, in **Chapter 4** we investigated whether 3D motion stimuli were able to cause a larger visual-vestibular conflict compared to 2D stimuli. To that end, participants viewed the same motion stimulus as used in **Chapter 3** in both 2D and 3D, and again VIMS and postural sway were studied.

Based on the MST, it is next expected that especially visual cues containing information about Earth-verticality influence the visual-vestibular conflict, thus also influence the CNS workings. More specifically, Earth-fixed visual cues (e.g. the edges of a TV-screen) are predicted to result in a better alignment of the expected vertical ($\mathbf{u'}$) and expected sensed vertical ($\mathbf{u_s'}$) with the Earth-vertical, resulting in smaller responses to visual motion stimuli. However, how influential these visual Earth-fixed cues really are is a question that has not yet been experimentally addressed. The main objective of **Chapter 5** was, therefore, to scrutinize the effect of an Earth-fixed visual manipulation (i.e. Earth-fixed frame), presented together with roll-motion around the line of sight, on postural sway, the SVV, and VIMS.

In **Chapter 6** we approached the internal mismatch from a different angle. As discussed earlier, a maladapted internal model of verticality could also lead to internal mismatches, which are hypothesized to be the underlying cause for the symptoms experienced by visual-vestibular mismatch (VVM) patients. Moreover, a core prediction is that these patients are more sensitive to a visual-vestibular conflict than controls. This would manifest itself in larger increases in motor and perceptual symptoms compared to controls when exposed to visual motion. In **Chapter 6** we thus tried to answer the question whether VVM patients possess a maladapted internal model of verticality and whether visual motion plays an essential role in triggering VVM symptoms. To that end, postural sway, the SVV, and VIMS were measured in these patients and in age-matched healthy controls before, during and after exposure to a stimulus, again rotating around the line of sight, and before, during and after exposure to a stationary stimulus.

Finally, a manipulation that has often been used to modulate a visual-vestibular conflict is the perceived depth order, also called fore-background segregation[69–71]. Intuitively, one could reason that visual factors related to this fore-background segregation, such as stimulus size and the number of objects (density), can differentially influence the visual vestibular conflict. In **Chapter 7** we thus asked whether varying the density would interact with the fore-background segregation in the modulation of the visual-vestibular conflict. We hypothesized that increasing the density in the background pattern would increase the visual-vestibular conflict to a greater extent, compared to an increasing the density in the foreground pattern. Because previous research has shown that postural sway and vection – an experience of self-motion while being physically stationary – are affected in a similar way during exposure to visual motion, suggesting a common neural mechanism[32,60,72], we included postural sway and roll-vection as the motor and perceptual responses. Both variables were investigated during exposure to stimuli rotating around the line sight in which the amount of objects perceived in the fore- and background were systematically varied.

In table 1.1 an overview of the research questions addressed in **Chapters 2** to **7** is presented. Finally, in **Chapter 8**, the findings from **Chapters 2** to **7** will be integrated and reflected upon from a theoretical, as well as from an applied perspective.

Table 1.1. Overview of the research questions addressed in the following chapters.

Chapter	Manipulation	Research question
2	Visual motion	Is visual motion in visual stimuli necessary to induce a visual-vestibular conflict?
3	Stereoscopic 3D	Does viewing a stereoscopic 3D movie in a cinema cause a visual-vestibular conflict ?
4	Stereoscopic 3D versus plain 2D	Does viewing a stereoscopic 3D exacerbate the visual-vestibular conflict, compared to 2D viewing?
5	Visual Earth-fixed cues	Do visual Earth-fixed cues suppress the visual-vestibular conflict?
6	Visual motion	Do VVM patients possess a maladapted internal model? Does visual motion play an essential role in triggering VVM symptoms compared to healthy contols?
7	Fore-background segregation combined with number density	Does the number of objects interact with the fore-background segregation in the manipulation of a visual-vestibular conflict?