Standing Well

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Chapter 8

Summary and discussion

8.1. Summary

The aim of this thesis was to 'open the neural black box', i.e. the central nervous system (CNS), and examine its workings during a visual-vestibular conflict. To induce a visual-vestibular conflict I focussed on various manipulations of visual stimuli, whereas the vestibular cues were not manipulated; thus, while keeping the participants upright. In this thesis it is proposed that the CNS workings during a visual-vestibular conflict include an internal model of verticality, as is proposed by the motion sickness theory (MST). More specifically, a visual-vestibular conflict is thought to cause an internal mismatch between the actual body state, that is, postural orientation and sensory cues on the one hand, and its neural representations as provided by an internal model of verticality on the other. I assume these internal mismatches to affect specific motor and perceptual responses. In order to reveal the workings of the CNS during a visual-vestibular conflict, the patterns of these motor and perceptual responses were monitored. The studied motor and perceptual responses included postural sway, the subjective visual vertical (SVV), visually induced motion sickness (VIMS), and in one study also roll-vection.

In a first attempt to examine the conditions under which a visual-vestibular conflict can be induced, we focussed on one crucial aspect of visual stimuli: the presence or absence of visual motion. 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. However, the perhaps obvious contrast with static visual stimuli (with the same content) had never been tested. Thus, it was unclear whether motion is both a necessary and a sufficient condition to induce a visual-vestibular conflict. To that end, in **Chapter 2** we exposed participants to motion and still images, adapted from a popular first-person shooter game, in separate sessions. Before, during, and after exposure, participants rated their VIMS symptoms, and data on postural sway was obtained using a force platform. Postural sway was characterised by both global parameters and parameters related to the correlational structure of the centre of pressure time series. Results showed, in line with existing literature, that VIMS scores were significantly increased directly after exposure to the motion images, but not by the still-images. However, to our surprise, postural sway was significantly increased after exposure to both motion- and still images, which suggests that motor responses are (partly) dissociated from VIMS effects during a visual-vestibular conflict. Possibly, the equal increases in postural sway were caused by visual effects that were present in both still and motion images. Concluding, these results showed that VIMS symptoms and postural parameters are not similarly affected by viewing visual motion stimuli.

Next, in **Chapter 3** we investigated the influence of another visual manipulation on the visual-vestibular conflict: stereoscopic 3D.

With its increasing popularity, the public health concern that viewing 3D motion stimuli causes significant adverse effects is growing. Moreover, 3D is proposed to potentially cause more adverse effects compared to viewing 2D due to a more pronounced visual-vestibular conflict. To that end, in **Chapter 3** we first studied whether viewing a 3D motion stimulus caused an increase in VIMS and postural sway. Participants viewed a 3D documentary in a cinema, where we obtained data on VIMS and postural sway before and after the exposure. A significant increase in VIMS as well as in postural sway was observed after exposure as compared to before; which we ascribed to a visual-vestibular conflict that influenced both VIMS and postural orientation. However, in this experiment we were not able to include a condition in which participants viewed the same stimulus in 2D. The question whether viewing 3D motion stimuli would cause a larger visual-vestibular conflict, resulting in more VIMS and postural sway as compared to viewing 2D stimuli, was thus left open. No other study had yet addressed this question.

In order to fill this knowledge gap, in **Chapter 4** we used an experimental design including a 2D and a 3D condition in which participants watched the same motion stimulus as in **Chapter 3**. For practical reasons a commonly available 55 inch TV-screen was used to display the motion stimuli. We expected that 3D motion stimuli would cause a larger visual-vestibular conflict compared to 2D stimuli, because of their increased naturalness. Again, participants rated their VIMS symptoms, and we obtained data on global and structural parameters of postural sway. To our surprise, VIMS reports revealed that after both 2D and 3D exposure viewers only experienced mild oculomotor and disorienting symptoms, without substantial nausea, as was observed in the cinema (**Chapter 3**). Moreover, postural sway was significantly and equally increased after viewing both 2D and 3D stimuli. This seems to suggest that stereoscopic 3D stimuli do not necessarily cause a larger visual-vestibular conflict, as inferred from the VIMS results and postural parameters, compared to viewing 2D stimuli. The lack of difference can be explained by the fact that the 3D-effects in this documentary were optimized for viewing in a cinema (as in **Chapter 3**), whereas the projection on the TV-screen (as in **Chapter 4**) caused quarantining of the visual input; in other words, the visual input was set aside by the CNS.

As outlined in **Chapter 1**, especially visual cues that contain information about Earth-verticality, i.e. Earth-fixed cues, are proposed to suppress the influence of visual motion on a visual-vestibular conflict. Yet, no study had experimentally addressed the question how influential these visual Earth-fixed cues really are. In **Chapter 5** we therefore aimed to unravel the effect of an Earth-fixed visual manipulation, presented together with roll-motion around the line of sight, on a visual-vestibular conflict by measuring motor and perceptual responses. We exposed participants to visual roll-motion, with and without an Earth-fixed frame, while obtaining data on postural sway, the SVV and VIMS symptoms. Results showed that the presence of a visible Earth-fixed frame consistently decreased the effect of the visual roll-motion on postural sway, SVV deviations and VIMS symptoms. These findings thus showed that, as hypothesized, a visual Earth-fixed cue can significantly reduce a visual-vestibular conflict and the respective motor and perceptual effects caused by roll-motion. Moreover, the observation that all motor and perceptual responses were affected in a similar way by an Earth-fixed cue and roll-motion, are an indication for a CNS working mechanism that resembles characteristics of the MST, as I will elaborate on further below.

In **Chapter 6** we approached the internal mismatch from another direction by examining a poorly understood group of patients that regularly report aggravation of vestibular symptoms (such as postural unsteadiness and nausea) by visual stimuli, often without a clear neurological cause. Individuals with such symptoms are known as visual-vestibular mismatch (VVM) patients. We first aimed at getting a better insight into the underlying neural mechanism of VVM by examining the same motor and perceptual responses as studied in **Chapter 5**: postural sway, the SVV and VIMS. Second, we investigated whether motion around the line of sight is a necessary condition to aggravate their motor and perceptual symptoms, or whether a stationary visual stimulus would provoke equal increases in VVM symptoms. We exposed VVM patients and age-matched controls to a visual pattern that rotated around the line of sight in one session, and in another session to the same, but stationary, pattern. A first finding was that patients always swayed significantly more and reported more severe VIMS symptoms than the healthy controls, irrespective of the stimulus type they were exposed to. Secondly, VVM patients and controls both exhibited an increase in postural sway and VIMS after prolonged exposure to roll-motion, while the SVV was not affected. Only the VVM patients, however, reported significantly higher VIMS scores after exposure to roll-motion compared to scores after exposure to a stationary stimulus. Despite the large variability observed, and a rather inhomogeneous patient group, these findings showed that VVM patients do differ from healthy controls on motor and perceptual responses and that visual roll-motion is a crucial factor in aggravating VVM symptoms. A possible explanation for these findings is a persistent neural visual-vestibular integration deficit that leads to inaccurate neural representations, which are responsible for the observed VVM symptoms. Yet, further research should focus on unravelling the exact underlying neural mechanisms and deficits.

Finally, in **Chapter 7** we investigated the effect of another visual manipulation on the visual-vestibular conflict: the depth order, also called fore-background segregation. Intuitively, one would expect that visual factors related to this fore-background segregation, such as stimulus size and object density, are able to differentially influence the visual-vestibular conflict. More specifically, we assumed that if a visual factor belonging to the background is present in the background pattern, it would increase the visual-vestibular conflict; while it would suppress the visual-vestibular conflict when presented in the foreground. Based on the observation that the number of objects (density) under normal circumstances differs between the fore- and background, we asked whether varying the density would interact with the fore-background segregation in the modulation of the visual-vestibular conflict. To that end, we included postural sway and roll-vection as the motor and perceptual responses to be studied. Moreover, previous research has shown that these responses are affected in a similar way during exposure to visual motion, suggesting a common neural mechanism. We therefore measured postural sway and roll-vection during exposure to stimuli rotating around the line of sight, while varying the object density in the fore- and background. Results showed that, as expected, the density interacted with the fore- and background segregation in the modulation of both postural sway and roll-vection. Based on these results, we concluded that the ratio between the densities of the fore- and background patterns is an important factor in the interaction with the fore-background segregation, and not the density of the rotating pattern per se. More specifically, when a rotating background contained more objects (to a certain maximum) than the static foreground a larger visual-vestibular conflict was evoked, resulting in longer vection and more postural sway, compared to a rotating foreground with more objects than the static background. Finally, the finding that postural sway, as well as vection were modulated in a similar way, provided new evidence for a common neural origin regulating both postural sway and vection.

Table 8.1 on the next page provides an overview of the research questions, examined variables and significant findings reported on in **Chapters 2 to 7**.

Chapter	Research question	Findings
2	Is visual motion in visual stimuli necessary to induce a visual-vestibular conflict?	VIMS: ↑ only in motion condition. Postural sway: ↑ in motion and no-motion condition, with motion = no motion.
3	Does viewing a stereoscopic 3D movie cause a visual-vestibular conflict ?	VIMS: ↑ Postural sway: ↑
4	Does viewing stereoscopic 3D exacerbate the visual-vestibular conflict, compared to 2D viewing?	VIMS: ↑, equal for 2D and 3D. Postural sway: ↑, equal for 2D and 3D.
5	Do visual Earth-fixed cues suppress the visual-vestibular conflict?	VIMS: ↑ only without Earth-fixed cues Postural sway: ↑ only without Earth-fixed cues SVV: ↑ only without Earth-fixed cues
6	Do VVM patients (P) possess a maladapted internal model? Does visual motion play an essential role in triggering VVM symptoms compared to healthy controls (C)?	VIMS: always P > C . For P and C Motion > No motion Postural sway: always P > C. For P and C Motion > No motion SVV: P = C. For P and C Motion = No motion
7	Does the number of objects interact with the fore-background segregation in the manipulation of a visual-vestibular conflict?	Postural sway: Back > Fore and higher density caused larger postural sway. Back+Density > Fore+Density Vection: Back > Fore and higher density caused more vection. Back+Density > Fore+Density

In the remainder of this chapter, the findings on postural sway and VIMS from the previous chapters will be combined and reflected upon from a theoretical perspective, with a focus on the main aim of this thesis, that is, examining the CNS workings during a visual-vestibular conflict. Besides a theoretical reflection, I will also discuss these findings from an applied point of view. Furthermore, I will organise this discussion per response, starting off with the findings regarding postural sway. Second, the results regarding VIMS will be discussed. Third, I will combine the findings on postural sway and VIMS and discuss how these results add to the knowledge on what happens in our "neural black box", i.e. the CNS, during a visual-vestibular conflict. Finally, this chapter will be concluded with directions for future research.

8.2. Endogenous and exogenous effects on postural sway

By using a force platform we obtained insight into postural excursions, also called postural sway, suggested to contain information about how the CNS controls body orientation. As explained in **Chapter 1**, postural sway is known to be affected in an endogenous manner (as can be inferred from an after-effect), as well as in an exogenous manner (typically momentary) by a visual-vestibular conflict. First, I will elaborate on the postural sway findings obtained with eyes closed, followed by the findings obtained with eyes open. Second, I will discuss how these findings add to the knowledge on CNS processes at work during a visual-vestibular conflict. Finally, I will elaborate on some practical implications of these results.

In **Chapters 2, 3** and **4** we obtained postural sway with eyes closed in order to get more insight into the influence of a visual-vestibular conflict on CNS workings. First, in **Chapter 2** we investigated whether visual motion was a necessary and sufficient condition to induce a visual-vestibular conflict. Second, in **Chapters 3** and **4** we aimed to get insight into a visual-vestibular conflict caused by stimuli containing stereoscopic 3D cues, and whether viewing 3D stimuli evoked a larger conflict compared to viewing 2D stimuli, respectively. We expected to induce a larger conflict, and thus to find a larger increase in postural sway, when participants were exposed to motion images compared to still images (**Chapter 2**) and when they viewed 3D motion pictures in comparison to 2D motion pictures (**Chapters 3** and **4**). To our surprise, we observed that postural sway was always increased after exposure, irrespective of variation in visual manipulations. This finding is further supported by Fig. 8.1, in which the results of **Chapters 2** and **4** on postural sway are grouped together. Exposure to visual stimuli always caused equal increases in all conditions. Summarized, we found no differential effect of any of the visual manipulations on postural sway obtained with eyes closed.

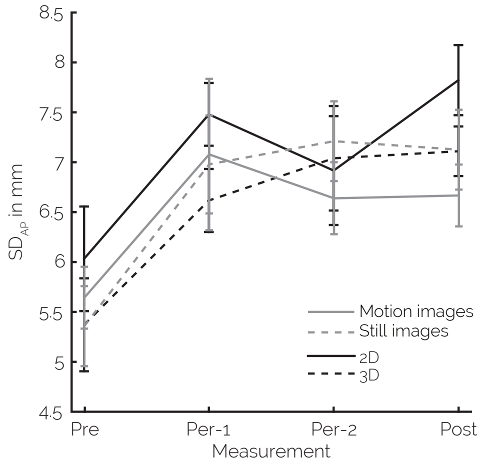

Figure 8.1. Standard deviations of sway in antero-posterior directions, of Chapter 2 and Chapter 4 combined. In both chapters postural sway increased due to exposure to visual stimuli, irrespective of the visual manipulation.

Yet, in **Chapters 5** and **7**, in which postural sway was obtained during exposure with eyes open, we did observe a differential effect of the visual manipulations on postural sway. A visual Earth-fixed frame significantly decreased postural sway during exposure to roll-motion (**Chapter 5**), and increasing the density of a rotating pattern had a larger effect on postural sway when the rotating pattern was perceived in the background compared to the foreground (**Chapter 7**). Moreover, in **Chapters 5** and **6** we observed that visual motion is able to influence postural sway, i.e. postural sway was significantly increased during exposure to a rotating stimulus compared to a stationary stimulus. So, in contrast to the findings in **Chapter 2**, visual motion can have an effect on postural sway, but only in an exogenous manner. Several other studies substantiate these findings in which significant increases in postural sway due to exposure to a stimulus in roll compared to a stationary stimulus were reported[60,72,192,193]. Moreover, just as visual (roll-) motion only had an exogenous influence on postural sway, also stereoscopic 3D motion pictures have shown to differentially affect postural sway in a direct way. In one study, larger postural excursions were observed during exposure to motion pictures displayed in stereoscopic 3D, compared to 2D motion pictures[74]. Thus, a first important conclusion that can be drawn from these studies is that postural sway can be affected by visual manipulations in a direct, exogenous way, i.e. with eyes open during exposure to visual motion.

Although we cannot directly conclude from these findings whether postural orientation is driven by an internal model of verticality as suggested in the introduction, these and other results (as discussed in **Chapter 5**) do provide evidence in favour of an internal model of verticality to control postural orientation[11,12]. As regards the MST, we hypothesized that postural orientation is driven by the difference in orientation of the expected vertical (**u'**) and the body axis (**u**). Results from **Chapters 5** and **7** indeed showed that postural sway obtained during exposure to visual roll-motion was differentially affected by visual manipulations. Therefore, I argue that postural sway obtained in these studies does provide insight into the difference between the orientation of expected vertical (**u'**) and actual body axis (**u**) during a visual-vestibular conflict. First, a visual Earth-fixed cue reduced postural excursions (**Chapter 5**), thereby indicating that Earth-fixed visual cues facilitate (an upright) postural orientation (less variability and lean). Second, we observed that the dot pattern density interacted with the depth order in the modulation of postural sway (**Chapter 7**). This finding suggests that it is especially motion perceived in the background that is used to control postural orientation. Since Earth-fixed cues are tightly related to the background in an ecological sense, both findings from **Chapters 5** and **7** substantiate that cues related to the "Earth-fixed" background, specifying the Earth-vertical, are important in the regulation of postural orientation. Accordingly, these findings suggest that the CNS uses Earth-vertical information in the regulation of postural orientation; thus making an internal model of verticality, such as incorporated in the MST, a plausible CNS working mechanism for postural control.

Despite that the visual manipulations did not have a differential effect on postural sway in **Chapters 2, 3** and **4**, the finding that postural sway was significantly increased after exposure in all experiments points towards a difference between the expected vertical (**u'**) and actual body axis (**u**). Interpreting the increases in postural sway from **Chapters 2, 3**, and **4** as a result of the difference between **u** and **u'**, suggests that the expected vertical (**u'**) became less accurate, i.e. deviated more from the body axis (u) due to exposure to an altered visual environment per se. Put simply, motion pictures caused a general degradation of postural orientation due to larger discrepancies between the actual body axis (**u**) and the expected vertical (**u'**).

However, it can be questioned whether the observed increases in postural sway obtained with eyes closed were solely caused by a deviation of the expected vertical (**u'**). Because we did not observe a differential effect of any of the visual manipulations on postural sway, I propose that this general increase not only reflects a change of the expected vertical (**u'**), but is mainly the result of other neural processes that modify the way we control our posture[209]. It has been proposed that the CNS may increase postural sway on purpose to gain more sensory information on a larger scale[27,210]. An increase in postural sway therefore does not have to reflect a deviation of the expected vertical (**u'**), but could also serve an exploratory purpose[27,210], which I suggest is what we have observed in **Chapters 2, 3** and **4**.

Finally, one could question whether just sitting quietly in between measurements may have influenced postural sway. A large amount of studies have investigated the effect of time on centre of pressure (CoP) variables, including the variables examined in this thesis. A review of the literature on the test-retest reliability of CoP measurements revealed that the overall reliability of CoP parameters is acceptable ($r \geq .75$) with a sufficient repetitions and sampling duration[211]. In 2009 a study was performed on the effect of trial repetition with 1 min rest intervals, in which the participants were seated, for several CoP parameters also used in this thesis[212]. Results showed that the reliability of the CoP parameters increased with each repetition and from three trials the correlation for all parameters were above 0.75, indicating a good correlation[212]. Stated differently, these findings indicate that without exposure postural parameters do not significantly vary when at least three trials are performed. Based on these findings, it seems unlikely that the changes in postural sway found in the experiments was due to just sitting still.

By exposing participants to visual stimuli, it became more difficult to use visual cues to regulate body orientation, accordingly introducing an altered relationship between the participant and the visual environment. By increasing postural sway, participants boosted the availability of sensory information to regulate postural orientation and to discover this altered relationship[27,134,210]. Thus, exposure to a virtual environment per se seemed to be more influential than the visual manipulations, resulting in postural behaviour of an exploratory nature. The results regarding the structural, fractal properties of postural sway obtained in **Chapters 2** and **4**, are in line with this explanation. The structural parameters of postural sway revealed that especially the short-term, i.e. high-frequency, characteristics were elevated in all conditions affected by exposure to motion pictures. More specifically, on a short time scale it became more likely that postural excursions continued with the same – or increasing – speed in the future as they did in the past. These high-frequency changes are assumed to reflect fast, automatic postural excursions outside conscious awareness209, that could enable the CNS to gather more sensory information about the interaction with the virtual environment.

From a practical perspective these findings underpin the importance of the way changes in postural control due to a visual-vestibular conflict are measured. More specifically, obtaining data on postural orientation during and directly after a visual-vestibular could provide a more complete insight into the CNS workings. Therefore, it would be interesting to obtain postural sway measurements during and after a visual-vestibular conflict to examine the exogenous, as well as the endogenous influence of the visual-vestibular conflict on postural sway.

Finally, the findings on postural sway from **Chapter 6** show that postural sway could be an objective parameter in studying the influence of visual motion on, e.g. visual-vestibular mismatch (VVM) patients. There we observed that the postural excursions of VVM patients were always significantly increased compared to healthy controls. A decrease in these postural excursions during rehabilitation could therefore point towards a positive effect of rehabilitation or treatment.

8.3. VIMS

VIMS was studied in **Chapters 2** to **6**. In **Chapters 2, 3** and **4** participants were exposed to visual stimuli containing motion in all degrees of freedom, while in **Chapters 5** and **6** participants watched roll-motion around the line of sight. As explained in **Chapter 1**, based on the MST, it was assumed that VIMS was caused by an internal mismatch between the sensed vertical ($\mathbf{u_s}$) and the expected sensed vertical ($\mathbf{u_s'}$).

First, in **Chapters 2, 5** and **6** we hypothesized that visual motion was necessary to induce VIMS, which indeed appeared to be a crucial factor. Thus, we can conclude that visual motion spanning a large part of the visual field seems to be necessary to induce a visual-vestibular conflict that leads to VIMS. **Chapter 5** also showed that, as hypothesized, visual motion with respect to the Earth-vertical is a provocative factor for VIMS, and that visual Earth-fixed cues suppress the provoking effects of visual roll-motion. Bos et al.[2] argued that visual patterns with a clear tilted Earth-fixed texture can influence the expected sensed vertical ($\mathbf{u_s'}$), In **Chapters 2, 5** and **6** the visual stimuli suggested a tilt of what is visually perceived as vertical away from the Earth-vertical, thereby causing a deviation the expected sensed vertical ($\mathbf{u_s'}$) and an internal mismatch that led to VIMS. Thus, viewing motion that suggests a tilt of what is visually perceived as vertical, induced an internal mismatch that expressed itself through VIMS. Moreover, **Chapter 5** also provided evidence that Earth-fixed cues can improve the precision of the expected sensed vertical ($\mathbf{u_s'}$) with respect to the Earth-vertical, reducing the internal mismatch, and thus again, VIMS. The Earth-fixed frame described in **Chapter 5** provided a veridical visual Earth-fixed cue, that resulted in smaller deviations of the SVV, that is thought to be highly dependent on the output of the internal model of verticality. We can therefore conclude that presence of the Earth-fixed frame increased the accuracy and precision of the output of the internal model, thus leading to less sickness. In summary, the findings of **Chapters 2** and **5** have provided evidence in favour of CNS workings that reflect an internal model of verticality, as incorporated in the MST.

In addition, we hypothesized that the influence of a visual-vestibular conflict could be enhanced by stereoscopic 3D cues. In **Chapter 3** we observed that participants reported significant VIMS symptoms after viewing motion pictures in stereoscopic 3D at the cinema, which is in line with earlier studies[15,17,55–57]. In all these studies participants reported a significant increase in VIMS due to exposure to a 3D motion stimulus. Moreover, several studies showed that a 3D motion stimulus caused more VIMS compared to a 2D stimulus[15,17,55,56]. In **Chapter 4**, we therefore expected that the 3D motion pictures would cause the same level of sickness as observed in

Chapter 3, when shown on a TV screen. Furthermore, we hypothesized that participants would experience more sickness when the motion pictures were shown in 3D compared to 2D. However, the documentary only caused mild symptoms in **Chapter 4**, irrespective of viewing it in 2D or 3D.

This comparison raised the question why the documentary was not able to elicit the same amount of VIMS when shown on a television, as it did in a cinema. As discussed in **Chapter 4**, two factors regarding the use of a TV screen are suggested to have supressed VIMS. In **Chapter 4**, the TV screen size was significantly smaller compared to the cinema screen used in **Chapter 3**, causing both geometrical distortions[130,131] and a large difference between the viewing angle captured by the camera and the viewing angle subtended by the TV-screen[35,47]. These two factors may have caused a phenomenon called quarantining. Visual cues that are obviously incongruent to other (vestibular) cues are proposed to be set aside by the CNS; in other words, the visual cues are quarantined[107,132]. Quarantining can thus decrease or even eliminate the visual-vestibular conflict, and therefore is a situation that can be added to the situations described in Fig. 1.3 in **Chapter 1** (Fig. 8.2). Due to quarantining of the visual cues the sensed vertical (us) mainly relies on correct vestibular cues, reducing the internal mismatch with ($\mathbf{u_s'}$), with less or no VIMS as a result. Put simply, quarantining suppressed an internal mismatch which resulted in less VIMS than hypothesized when viewing cinema motion pictures on a TV screen (Fig. 8.2). However, it may be the case that the viewer still exhibits increased postural excursions. This topic will be addressed in the next section, in which the findings on postural sway and VIMS are combined. Summarized, these findings do provide evidence in favour of the MST, but also revealed that other processes, such as quarantining, can attenuate the visual-vestibular conflict, the internal mismatch and VIMS.

#	situation	u	u_s	u'	u_s'
5.	Quarantining				

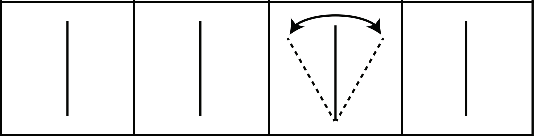

Figure 8.2. A schematic representation showing the effect of quarantined visual motion on the average orientation of the body axis (**u**), the sensed vertical ($\mathbf{u_s}$), the expected vertical (**u'**) and the expected sensed vertical ($\mathbf{u_s'}$). See text for full explanation.

From a practical perspective, these findings provide valuable information that can help in the design of motion pictures for, e.g. entertainment purposes and in the design of optokinetic stimuli used for vestibular rehabilitation. In the entertainment industry VIMS is an adverse side effect that designers and researchers have tried to reduce by adding several visual features, such as a virtual nose[213] or a static dot positioned in the centre of the screen[79]. The findings from **Chapter 5** show that it is especially important to add veridical Earth-fixed cues to the motion pictures that reflect the visual environment or background. In this view, interestingly, adding a nose to motion pictures moving with the head (-mounted display) is not the best possible solution. The nose can be perceived as part of one's own body and does not provide any visual information regarding the Earth-vertical. Placing a dot in the centre of the screen, as provided by the video game Mirror's Edge[79], would not be effective either. The dot does not contain any veridical Earth-fixed information and has object-specific characteristics, such as a small relative size, compared to the virtual scene. Therefore, it is likely that it is not perceived as part of the background, but as an object partially occluding the virtual background. Moreover, based on the findings from **Chapter 7**, the dot could perhaps even increase an internal mismatch and hence VIMS, because it creates a clear depth order. Based on the findings from **Chapters 5** and **7**, I propose that the addition of a visual Earth-fixed cue that is perceived as part of the background is most effective in suppressing VIMS. As an example, the Earth-fixed frame of the screen could be emphasized , resembling the Earth-fixed frame used in **Chapter 5**.

In designing optokinetic stimuli for rehabilitation purposes, the findings of both **Chapter 5** and **Chapter 7** are also valuable. In vestibular rehabilitation, personalized exposure to challenging motion is advised[64]. Visual Earth-fixed cues, as well as variation in depth-order and density could be used to create customized exposure.

8.4. One internal model with multiple outputs

As outlined in **Chapter 1**, the aim of this thesis was to get more insight into the workings of our "neural black box" during a visual-vestibular conflict. It was hypothesized that the CNS incorporates an internal model of verticality, as included in the motion sickness theory (MST). The MST proposes that postural sway and VIMS are controlled by two separate outputs of the internal model of verticality: the expected vertical (**u'**) and the expected sensed vertical ($\mathbf{u_s}$**'**), respectively[1,2]. The assumption that these two responses are driven by separate outputs allows differences between the patterns of postural sway and VIMS during a visual-vestibular conflict. An obvious question is therefore whether, and to what extent, the observed responses behaved in a similar manner. Interestingly, comparison of postural sway and VIMS revealed that these responses were indeed not always affected in a similar way. Postural sway and VIMS were recorded together in **Chapters 2, 3, 4, 5** and **6**, and thus allowed us to use their patterns to get more knowledge on what happens in the "neural black box" during a visual-vestibular conflict. Hereby it has to be noted that we considered postural sway obtained with eyes open and eyes closed both to be at least partly regulated by the expected vertical (**u'**).

In three studies, presented in **Chapters 3, 5** and **6**, we observed that postural sway and VIMS were similarly affected by the visual manipulations. In **Chapter 3**, participants exhibited an increase in both VIMS and postural sway due to exposure to 3D motion pictures. In **Chapter 5**, we also observed that postural sway and VIMS were affected in a similar way by two visual manipulations, roll-motion and an Earth-vertical cue. Also in **Chapters 2** and **6** participants exhibited an increase in postural sway and VIMS due to exposure to visual motion. However, in **Chapter 2** in the condition with exposure to still images, we observed that postural sway and VIMS behaved differently. In this condition participants only exhibited an increase in postural sway, but they reported no increase in VIMS. Also in **Chapter 4** we observed that only postural sway increased, and again there was no increase in VIMS. We thus identified situations that caused an increase of both postural sway and VIMS, but also found situations that caused an increase in postural sway without the occurrence of VIMS.

The situations described above are all in line with the conditions as described by Bos[1]. Bos[1] nicely addressed several examples showing that postural sway and VIMS are in certain conditions similarly affected, but can also be dissociated. Many studies, including the studies discussed in **Chapters 2, 3, 5** and **6**, found that an increase in postural sway was accompanied by an increase in VIMS. Moreover, several studies even found correlations between postural sway and VIMS[76,93]. On the other hand, an increase in postural sway without an increase in VIMS has also been found in the current experiments (**Chapters 2** and **4**), and has also been repeatedly reported. For example, across multiple sessions VIMS severity has shown to decrease[50,214], while postural sway is been shown not to decrease, but even increase[214]. All these situations can be explained using the MST as shown by Bos[1]. To summarize, in some situations an increase of both postural sway and VIMS can be evoked, as we have observed in **Chapters 2,3, 5** and **6**; and an increase of postural sway without the occurrence of VIMS (as has been found in **Chapters 2** and **4**) which all fit within the MST. In other words, postural sway and VIMS may behave differently, while being mediated by one internal model.

8

However, one would ask whether there is more than only a "relatively" simple model at work during a visual-vestibular conflict. The results in this thesis indeed showed that other neural processes and factors can significantly influence our motor behaviour and perception (Fig 8.3). As regards postural sway, it was observed that motion pictures influenced postural sway obtained with eyes closed differently from postural sway with eyes open. The increased postural sway (with eyes closed) could have been caused by an exploratory neural mechanism that tried to obtain more sensory information (proproceptive and vestibular). The large amount of sensory information could be used by the CNS to establish the relationship with the environment. Thus, also other neural processes can influence our motor behaviour, and the motor behaviour itself can also close the perceptual-motor loop by increasing the magnitude of sensory signals from the other senses (Fig. 8.3). Moreover, this reasoning adds to the arguments provided by Bos[1] that an increase in postural sway is not a necessary and sufficient condition to experience VIMS, as is proposed by Riccio and Stoffregen[103].

The postural instability theory of Riccio and Stoffregen[103] is a well-known theory that also takes postural control as a starting point, just as the MST does. This ecologically based theory states "that animals become sick in situations in which they do not possess (or have not yet learned) strategies that are effective for the maintenance of postural stability" (p. 195) [103], and that "postural instability precedes the symptoms of motion sickness, and that it is necessary to produce symptoms." (p. 205)[103]. So, the question is whether the postural instability theory could explain the findings presented in this thesis.

First, based on the comparison of the findings on VIMS and postural sway from **Chapters 2, 3, 4, 5** and **6**, I conclude that the MST is better capable of explaining the findings presented in this thesis. We have observed that postural sway can increase without an increase in VIMS. Thus, increased postural sway appears not to be necessary to produce VIMS, as is proposed by the postural instability theory[103]. Yet, I conclude that VIMS and postural sway are related; however, the relationship is far more complicated than has been suggested by Riccio and Stoffregen[103.]

Second, we have observed in **Chapters 5** and **6**, in line with several other studies[31,215,216], that humans are able to align a visible line (SVV) in the dark very precisely and with little variation, with the Earth-vertical. If humans would not possess an internal model of verticality, the SVV would be mainly driven by sensory information. Considering that senses are known to be more susceptible to changes, such as noise and pathology, one would expect larger deviations and more variation of the SVV when it would only be controlled by sensory cues, than has been observed. In other words, the relatively small deviations and small variability observed in the SVV obtained in darkness, further support the hypothesis that the CNS adopts an internal model of verticality. In conclusion, these results can be explained with a theoretical framework that includes an internal model of verticality driving postural sway and VIMS, as is proposed by the MST.

Finally, whether or not one experiences VIMS from viewing stereoscopic 3D motion pictures, also seems to be greatly influenced by other (neural) processes such as quarantining (discussed in **Chapters 3** and **4**). Such neural processes could thus affect our perception and motor behaviour, possibly through changing the internal model of verticality (Fig. 8.3). Moreover, whether quarantining occurs seems to be dependent of environmental factors, such as the field of view or the type of stimuli used.

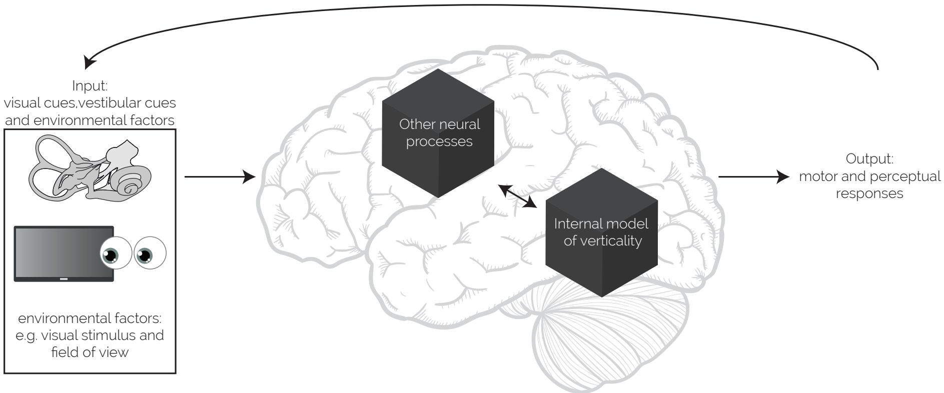

Figure 8.3. A schematic illustration of proposed interactions at work during a visual-vestibular conflict. The input that influenced the CNS processes also included, besides vestibular cues and visual cues, several environmental factors, such as the type of stimuli and field of view. These cues and factors provide input for an internal model of verticality and other neural processes. These other neural processes include for example quarantining and exploratory processes. These processes may have a direct influence on the output, but can also influence the output through the internal model of verticality. Moreover, the studied motor and perceptual responses can influence the sensory input, as with exploratory postural sway.

In summary, I conclude that by combining all findings presented in this thesis, we managed to take a "sneak peek" inside the "neural black box" during visual-vestibular conflict situations. This glimpse showed us that the studied motor and perceptual responses are plausibly driven by neural processes that embody an internal model of verticality, as incorporated in the MST. Thus, making the MST a plausible model reflecting the neural processes at work during a visual-vestibular conflict!

8.5. Roll-vection

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The reader familiar with the effects of a visual-vestibular conflict may think that I have omitted one important response that has been shown to be related to postural sway[60], as well as VIMS[61,62]. This response is vection, the sensation of self-motion while being physically stationary. Yet, we have decided not to include vection as a primary response, because of the following reasons.

First, when using stimuli containing motion in all degrees of freedom with no low frequency directional changes (as used in **Chapters 2** to **4**), it is difficult to induce vection. This type of motion pictures lack sustained, oscillating or unidirectional flow of the visual scene, which is needed to induce vection[87,88] (**Chapter 2**). To that end, vection measures were not included in **Chapters 2** to **4**. Second, self-reported vection measures may be confounded by other unusual sensations caused by exposure to visual motion, such as VIMS symptoms[217]. In **Chapters 5** and **6** we wanted to obtain the pattern of VIMS symptoms, and therefore decided not to include vection measures in these experiments.

In **Chapter 7** on the other hand, we aimed to examine the relationship between roll-vection and postural sway. Roll-motion around the line of sight, is known to cause a specific type of vection, here called roll-vection (**Chapter 7**). Roll-vection mainly comprises a sensation of static self-tilt instead of self-motion[63]. This tilt is thought to be the result of the internal mismatches that exists during exposure to roll-motion around the line of sight[2]. Although we have observed that roll-vection and postural sway changed in a similar way, we also observed that roll-vection is a difficult and rather subjective response to capture. More specifically, at the low densities, participants found it hard to report whether they experienced roll-vection or that they experienced other sensations, such as awareness of postural excursions. In addition, recently Palmisano et al.[217] have proposed that postural sway could be used in conjunction with vection measures to validate the vection measures. Summarized, vection is a response that is closely related to postural sway and VIMS, but because of our focus on postural sway and VIMS we decided not to include roll-vection as a primary response.

8.6. Future directions

The findings presented in this thesis are an invitation for future research into a fundamental, as well as an applied direction. I will first address opportunities for future fundamental research, followed by suggestions for applied research.

First, this thesis showed that in some instances postural sway and VIMS behave in a similar way, but not in all. Future research should therefore be devoted to find what causes sway and VIMS to behave similarly, or to cause them to be dissociated.

A second step towards further validating the CNS workings would be to focus on finding other motor and perceptual responses that primarily rely on the CNS workings of interest. In this thesis we chose postural sway as a response of interest, because it allowed us to study several properties of postural orientation. Instead of postural sway one could use the postural vertical, i.e. estimate of the orientation of the longitudinal body axis, which has been included in several other studies to assess the perception of verticality[11,38,218]. Although the postural vertical only gives insight into the perceived orientation of the body axis, while with postural sway multiple properties can be studied, it may be a response that relies more on the CNS workings of interest than postural sway.

Third, we have observed that environmental factors, such as the interaxial distance (distance between the lenses in a 3D camera) combined with the used displaying device (see **Chapters 3** and **4**), can have a significant influence on the internal mismatches and motor and perceptual responses

(Fig 8.3). Although we have provided insight into how these factors can influence motor and perceptual responses, future research should try to further unravel how these factors interact with the visual-vestibular conflict. For example, it would be interesting to examine how a visual stimulus recorded at different interaxial distances interacts with different displaying devices in the occurrence of a visual-vestibular conflict. Moreover, this approach could also indicate whether the interaction between the interaxial distance and the displaying device is indeed responsible for quarantining, as proposed in **Chapter 4**.

Finally, neuro-imaging techniques combined with behavioural and perceptual measurements can be a good approach to get more insight into the working mechanism adapted by the CNS during a visual-vestibular conflict. One could, for example, correlate SVV deviations or postural deviations with changes in cortical excitability of specific areas, so as to identify cortical areas that may be part of the CNS workings during a visual-vestibular conflict. An even more promising field that may be able to untangle the CNS workings during a visual-vestibular conflict is model-based cognitive neuroscience. This research field is based on a symbiosis of the concepts of formal modelling and cognitive neuroscience, and enables researchers to better understand the brain-behaviour relationship[219,220]. Though, the more difficult the computational model, the more difficult it is to validate the model with behavioural observations[219]. Therefore, to investigate the CNS workings during a visual-vestibular conflict, several hurdles have to be taken and several research fields have to collaborate. The first challenge would then be to create a mathematical model, that is less complex than the MST, to calculate how specific motor and perceptual responses will vary due to specific visual manipulations. Possible candidate responses may be the subjective visual vertical, or the postural vertical; and manipulations could for example include object density (as used in **Chapter 7**) or visual Earth-vertical cues (**Chapter 5**).

Summarized, although it will be a major challenge to understand the CNS workings during a visual-vestibular conflict, I do believe that if multiple research fields join forces we are able to further open the "neural black box" and see what happens inside during a visual-vestibular conflict!

From an applied perspective, we have provided insight into how visual manipulations can aggravate and attenuate the visual-vestibular conflict. However, more research is also needed, because of several practical reasons. First, virtual reality has not only a central role in the entertainment industry, but is also gaining ground in training and rehabilitation settings. So, more people are potentially exposed to a visual-vestibular conflict, which could lead to a larger incidence of adverse effects, such as nausea, perceptual distortions, and postural unsteadiness. Moreover, with the fast technological improvements, nowadays designers are able to achieve a better user presence in virtual environments, i.e. a sense of being there[221]. Although these improvements are aspired by designers, a higher user presence can be expected to elevate the impact of the visual-vestibular conflict, leading to more severe adverse effects. Summarized, more and more people find themselves more often in visual-vestibular conflict situations, that are becoming more provocative due to improvements in user presence.

The ultimate solution to distinguish adverse effects (due to elimination of a visual-vestibular conflict) and to maximize user presence, would be to include vestibular cues congruent with the visual cues. Several studies have already investigated the effects of combined visual- and vestibular stimulation by providing galvanic vestibular stimulation, and also the entertainment industry has taken a first step towards visual- and vestibular stimulation[222,223]. Research into how visual factors and manipulations aggravate or attenuate the motor and perceptual responses is thus needed to minimize unwanted effects and maximize desired effects. More knowledge on this topic could also give a boost to the use of virtual reality, because visual stimuli that suit specific requirements can be created when one knows how to maximize the desired effects with visual manipulations. For example, the entertainment industry could create motion pictures that increase the user presence by controlling the density in the fore- and background (as studied in **Chapter 7**). In vestibular rehabilitation, on the other hand, visual factors that gradually increase certain motor and perceptual responses, such as density (**Chapter 7**) or Earth-vertical cues (**Chapter 5**) could be used to provide a graded, personalized exposure to the patient.

Thus, although virtual environments will never get real themselves, there are more than sufficient reasons, and plenty of opportunities for future research, to make **Standing Well** in virtual environments reality!

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