

The Effects of Anxiety, Ageing, and Neurodegenerative Disease on Visual Reweighting for Postural
Control

A thesis submitted for the degree of Doctor of Philosophy

By

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EFFECTS OF POSTURAL THREAT ON VISUAL REWEIGHTING

Declaration

I hereby declare that this thesis has not been and will not be submitted in whole or in part to another University for the award of any other degree.

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Abstract

For most people, the complex mechanisms of sensory reweighting and maintaining balance are effective in maintaining relative automaticity and stability. However, this optimal function can be jeopardized by a range of factors. Ageing, anxiety, changes in attention, and neurodegenerative disease are some of the factors that potentially affect sensory integration for balance. These factors are explored in this thesis over several empirical studies using visual perturbations delivered using virtual reality. First, I examined the effects of ageing and anxiety on the postural response to the erroneous visual experience of self-movement (Study 1). Secondly, I explored these effects in the context of Parkinson's Disease with Freezing of Gait: a population with impaired non-visual sensory processing and increased anxiety related to motor control (Study 2). The final study attempts to isolate the effects of increased conscious control of movement on visual reweighting to examine the degree to which they account for the results of the previous studies (Study 3). Study 1 found that anxiety appears to relate to increased reliance on vision for balance, but it only partially accounts for greater reliance on vision in older adults. Study 2 found that people with PD+FOG take longer responding to the visual perturbation than healthy age-matched adults, and that freezing severity correlates with longer latency and possibly lower magnitude of response. Finally, Study 3 found no significant effect of increased conscious control of movement on reliance on vision for postural control. Overall, while anxiety does have the potential to increase reliance on visual input, increased visual dependency observed in older adults and people with PD is likely to have different origins, potentially related to physiological changes, rather than increased conscious control of movement. The General Discussion reviews the contribution of these findings to research on sensory integration and postural control, and discusses their implications, and directions for future research.

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Chapter 1. General Introduction (Literary Overview)

The most seemingly simple of tasks often require complex interactions between multiple systems in order to be performed smoothly. In humans, maintaining stable upright posture is one such function. This introductory chapter will first cover the basics of balance control, particularly regarding the different senses involved and how information from them is integrated to preserve a stable posture. This will be followed by an overview of the different (albeit non-mutually exclusive) factors that appear to affect sensory integration and postural behaviour, such as ageing, anxiety, and neurodegenerative disease. This overview, while acknowledging and describing previous work in the field, will also underline the current knowledge gaps in what we understand about how balance works in these contexts, and how the current thesis plans to address some of these questions.

Balance Control & Sensory Integration

The control of balance primarily relies on the function of the Central Nervous System (CNS), which must effectively integrate different sources of information from different sensory systems, such as the visual, vestibular, and proprioceptive systems (Della-Justina et al., 2015; Peterka, R. J., 2002). The vestibular system uses information from the semicircular canals and the otoliths in the inner ear to signal rotational movements and linear accelerations, which, together with visual information, tell us where we are in space and therefore what movements are needed to maintain a stable position (Angelaki & Cullen, 2008). Additionally, proprioception provides a sense of self-movement and body position through musculoskeletal signals; for example, the sensation of our feet on the ground (Stillman, 2002).

Paradigms using self-motion perception (for example, heading estimates) illustrate the concept of how the CNS integrates these different sensory inputs. On its own, unimodal presentation of sensory information (e.g., visual cues alone) allows some, albeit variable, estimation of self-motion. However, when different sensory cues are presented together, heading estimates become more accurate (Butler, Smith, Campos, & Bühlhoff, 2010; Butler, Campos, Bühlhoff, & Smith, 2011; Campos & Bühlhoff, 2012). This is commonly referred to as the redundancy phenomenon, whereby observers integrate multiple estimates that are weighted according to their respective reliability and yield more accurate estimates of self-motion than they would alone (Butler et al., 2011; Fetsch, Turner, DeAngelis, & Angelaki, 2009). For example, in a paradigm used by Butler et al. (2010) and Fetsch et al. (2009), observers were provided with both visual (optic flow depicting dots moving at varying angles through a virtual starfield on a large screen) and vestibular cues (being translated along heading directions at varying angles) in order to complete a heading discrimination task. In some trials, only one of the two cue types were available, and in others, both cue types were

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available. In some key trials, the cues were incongruent with each other, and their relative reliability was varied. Results demonstrated that heading estimates were significantly more accurate when both cue types were available, and that visual and vestibular cues were reweighted according to their perceived reliability in order to optimise heading estimation for balance control. Thus, accurate processing of sensory input and perception are necessary for effective motor control (Machado et al., 2010; Wolpert, Ghahramani, & Jordan, 1995). Furthermore, accurate perception also relies on motor actions such as active sensing (Kleinfeld, Ahissar, & Diamond, 2006; Wachowiak, 2011) and exploratory sway (Carpenter, M. G., Murnaghan, & Inglis, 2010). Meyer, Oddsson, and Luca (2004) demonstrated how the importance of foot cutaneous sensation for normal standing balance control is dependent on availability of other senses, whereby plantar sensation was demonstrably more useful for standing balance when participants had to close their eyes during bipedal stance.

It is evident, therefore, that motor control and multisensory processing are mutually interdependent (Gibson, 1966; Halperin, Israeli-Korn, Yakubovich, Hassin-Baer, & Zaidel, 2020; Prinz, 1997; Warren, 2006). Peterka (2018) describes a human balance control model that demonstrates how multiple sensory contributions are integrated and weighted to produce corrective motion. In this model, sensory inputs, from separate senses generated by current body sway angle (which may be produced by external stimuli such as visual surround tilt or support surface tilt), are integrated to form a “weighted summation of orientation information” (equalling to 1 when all senses are contributing). This estimate of body orientation is then compared with an internal reference, or “desired reference body orientation” (i.e., upright). If the internal estimate differs from the internal reference orientation, a sensory error is produced, which is transmitted to a “neural controller”. This controller then generates ankle torque, which, combined with passive torque generated by the body movement mechanics designed to keep the body in alignment with gravito-inertial forces, contributes to a corrective torque in the ankle. This corrective torque is proportionate to the amount of sensory error, which produces corrective body sway. This corrective motion then feeds back to the sensory inputs, and the process loops, providing ongoing corrective motion to keep the body in a stable position.

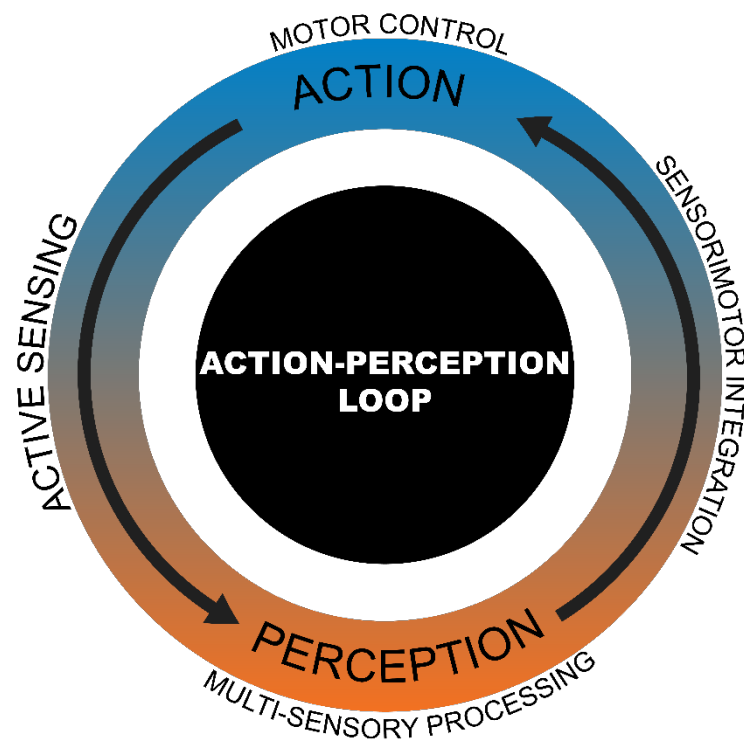


Figure 1. Visual depiction of the action-perception loop, adapted from Halperin et al. (2020).

While multiple sensory inputs are acquired and utilised to maintain effective balance control, these different senses are not necessarily weighted equally. Many researchers postulate that sensory reweighting in the brain occurs through a Bayesian estimation process, whereby the CNS reweights incoming sensory inputs based on their relative reliability, where more reliable inputs are upweighted (Bronstein, 2019; Butler et al., 2010; Knill & Pouget, 2004). One way to measure how much people rely on a particular sensory modality is to create an illusory difference between information acquired by separate senses and measure the postural responses. These manipulations can be classified as intra-modality or inter-modality. Intra-modality refers to changes that occur in one sensory modality due to a manipulation of input of that same modality, whereas inter-modality describes the effect on responses that occur in one sensory modality due to a manipulation of input of a different sensory modality (Saftari & Kwon, 2018).

In terms of vestibular sensory weighting, while previous research has found that vestibular weighting changes over different stages of dynamic movement (Bent, McFadyen, & Inglis, 2004), other experimenters have focused on static tasks and explored how the human postural system prioritises its reliance on visual, proprioceptive, or vestibular systems whilst in a static position. One of the earliest demonstrations of this type of task was done by Lee and Lishman (1975) who first utilised the “moving room illusion” to demonstrate the dominance of visual information in balance

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control. The authors used a small chamber suspended from the ceiling, whereby the walls could move while the participant remained still, presenting an illusory visual sensation of movement. This led to destabilisation of the participants' balance, indicating the strong influence of vision compared to information from lower limbs and vestibular input.

More contemporary methods have expanded on this line of research. For example, Keshner, Kenyon, and Langston (2004) exposed participants to either a moving support base (± 10 cm in the anterior-posterior direction), a moving visual field (± 3 m in a fore-aft motion, using a virtual reality delivered through stereographic goggles), or both at the same time. Postural response was measured via whole-body Centre of Mass (COM), and segmental movements were tracked using markers placed on the head, neck, femur, knee, and ankle, so that the movement and relative angular positions of each segment could be recorded. When each stimulus was presented by itself, the amplitude of postural response to either stimulus was relatively small. However, when they occurred simultaneously, the response to visual information was much stronger for the head and trunk movements and for the shank relative to either the visual or support base movement alone. Thus, the presence of a vestibular disturbance strongly potentiated the response to visual information – primarily, a large COM shift in the posterior direction in counteraction to the anterior visual perturbation. The authors argue that the brain does not ignore one input or another; rather, both are implemented in monitoring the environment, and subsequently affecting the body's response to its surrounds. However, when the incoming cues are at odds with each other, the ability to determine whether the movement is due to self-motion or environmental motion is impaired, and exteroceptive (e.g. visual) feedback is prioritised in order to respond appropriately to the changing external cues. Kabbaligere, Lee, and Layne (2017) found similar results when delivering conflicting proprioceptive (via an 80Hz vibration to the ankle) and visual (via optic flow in VR) stimulations. When applied separately, these stimulations elicited postural sway in opposing directions, with the proprioceptive stimulation eliciting backward shift in Centre of Pressure (COP) and the visual stimulation eliciting forward shift in COP. When applied together, a backwards sway was still elicited, but this was significantly reduced. This indicates that the presence of the conflicting visual motion moderated the extent of the proprioceptively induced postural response, and that the visual information received more “weight” in terms of reliability compared to the proprioceptive stimulation.

These findings were extended by Wang, Kenyon, and Keshner (2010), who varied the speed of a moving virtual visual scene (pitch-upward optic flow, giving the impression of tipping forwards) as well as tilting the floorplate support base (to a toe-up/dorsiflexion position giving the impression of tipping backwards) to measure postural reaction (whole body COM; measured via the sum of the

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movement several body segments, similar to Keshner et al. (2004)). In trials where only the visual scene moved, the scene was driven in the pitch-up direction at either 30°, 45°, or 60° per second. On a stationary support base, as the speed of the illusion increased, participants exhibited a counteracting backwards COM movement which increased in amplitude with the speed of the visual illusion. This effect was even stronger when the support base was tilted upwards (inclined at 30° per second for 30s in a toe-up position, then returned slowly to horizontal at 0.1° per second), which first elicited a forward COM shift in response to the support surface being tilted upward, followed by a corrective backward motion which increased in magnitude with the increase in visual scene flow velocity. These findings suggest that the control pathways for visual effects on posture are also utilised for postural sway elicited by the illusion of self-motion, and that vestibular input ambiguity leads to increased reliance on visual information to maintain an upright posture. These results are consistent with neurological findings that vestibular stimulation on its own causes activation of vestibular cortex areas with concurrent deactivation of visual areas, vice versa for visual stimulation on its own, while simultaneous stimulations of both senses produces activation in both areas (Deutschländer et al., 2002).

Relevance to Ageing

Evidence suggests that Older Adults (OAs) have greater difficulty maintaining stability both while standing and while walking (Hausdorff, Rios, & Edelberg, 2001; Horak, Shupert, & Mirka, 1989), and suffer from an increased likelihood of falls (Tinetti, Speechley, & Ginter, 1988). Previous research suggests a link between visual function decline and fall risk, but how these factors are connected has not been explicitly researched. One particular aspect of visual function that may be contributing to OAs' increased fall risk is visual motion perception, which strongly influences balance control and has been shown to be affected by ageing – as well as being an important aspect of sensory integration. A wealth of research suggests that optimal sensory integration (particularly during self-motion aspects of postural regulation) becomes somewhat impaired with age (Diederich, A., Colonius, & Schomburg, 2008; Ramkhalawansingh, Keshavarz, Haycock, Shahab, & Campos, 2016). For example, Choy, Brauer, and Nitz (2003) demonstrate that older adults show an increased reliance on visual information for balance control, whereby older women were less able to maintain a single-limb stance than younger women when instructed to close their eyes. As described above, the ability to reweight reliance on difference senses depending on their relative accuracy is an important factor of sensory integration for balance control. OAs seem to show more rigidity in dynamic sensory reweighting tasks compared to YAs, and tend to incorporate unreliable cues that may negatively affect their balance performance (Lich & Bremmer, 2014; Ramkhalawansingh, Butler, & Campos, 2018). For example, Dumas and Krampe (2010) demonstrated increased anterior-

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posterior sway in OAs compared to a younger group when exposed to inaccurate proprioceptive information that persisted even once the inaccurate sensory input was removed, indicating a less efficient sensory reweighting system in OAs compared to YAs. Eikema, Htazitaki, Konstantakos, and Papaxanthis (2013) suggest that, while OAs are often more reliant on visual information for balance control than YAs, they also find it difficult to downweight inaccurate proprioceptive input, either due to reduced sensitivity to proprioceptive cues, impairments in attention shifting (Hawkes, Siu, Silsupadol, & Woollacott, 2012), and/or impairments in cognitive motor prediction and planning (Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 2008). One study using functional Near-Infrared Spectroscopy (fNIRS) suggested that balance control in OAs requires more attentional capacity than in YAs (Lin, C., Barker, Sparto, Furman, & Huppert, 2017), and several others have demonstrated increased cognitive demands on OAs for balance control and compared to their younger cohorts (Kerr, Condon, & McDonald, 1985; Shumway-Cook, Woollacott, Kerns, & Baldwin, 1997; Shumway-Cook & Woollacott, 2000).

Anxiety could be one cognitive factor contributing to balance difficulties in OAs and increased risk of falls. There is a relatively high prevalence of anxiety about falling in OAs, occurring in between 12% and 85% of OAs (Legters, 2002; Scheffer, Schuurmans, van Dijk, van Der Hooft, & De Rooij, 2008). Known widely as Fear of Falling (FOF), this specific type of anxiety is strongly associated with an increased likelihood of falling (Hadjistavropoulos, Delbaere, & Fitzgerald, 2011), and can cause debilitating personal, social, and economic costs. Therefore, it is evident that exploring the effects of anxiety on sensory integration for balance control is an important avenue of research that may lead to improvements in our understanding of how we may reduce fall risk in vulnerable populations.

Neural Substrates of Balance Control & Anxiety

Under relatively non-stressful conditions, different sensory inputs are typically integrated in a way that maintains a stable balance. However, this is not always the case in conditions of heightened anxiety. A number of studies have examined the neurophysiological mechanisms through which anxiety influences postural control; anatomical studies describe how the areas of the brain that process and regulate anxiety (e.g. limbic system) and balance-relevant sensory information (e.g. parabrachial nucleus) are apparently connected. Research has uncovered some of the potential underlying neural substrates of the link between anxiety and visuo-vestibular circuits. While balance control in general is thought to directly involve the cerebral cortex (Bolton, 2015), the vestibular system in particular is reported to have bi-directional links to the parabrachial nucleus (PBN), which in turn projects out to the amygdala and autonomic/sympathetic nervous system.

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These areas form part of a network that processes incoming vestibular, somatic, and visceral input to mediate anxiety responses (Balaban, 2002). There also appear to be projections between the vestibular system and the caudal pole of the locus coeruleus (LC), which has been implicated as a starting point for anxiety responses and panic disorders (Aston-Jones, Rajkowski, & Cohen, 1999). The LC has also been suggested to be a modulator of vestibular function by mediating increases in postural sway and altered vestibular-evoked eye movements during stress-related arousal (Balaban & Thayer, 2001; Balaban, 2002). Furthermore, serotonergic and non-serotonergic connections are evident between the raphe nuclei and the vestibular system, as well as between the raphe nuclei and the LC (Furman & Lempert, 2016). Balaban (2002) suggests that this pathway contributes to the affective responses to unpleasant aspects of motion. This suggestion is supported by evidence that mood type and anxiety can alter balance performance (Bolmont, Gangloff, Vouriot, & Perrin, 2002). In clinical settings, the fact that selective serotonin reuptake inhibitors (SSRIs) can be effective in treating balance-related disorders such as vertigo provides further evidence for this link (Staab, 2014). Additionally, the common comorbidity of balance disorders and anxiety disorders, such as chronic dizziness and generalised anxiety (Staab & Ruckenstein, 2005), as well as in diseases such as Parkinson's (Ehgoetz Martens et al., 2017), provides further support for all these networks' roles in mediating the relationship between anxiety and postural control (Balaban, Jacob, & Furman, 2011). In fact, the degree to which anxiety and balance-related systems (particularly the vestibular system) are evidently so intimately connected, Staab, Balaban, and Furman (2013) argue that they should not be viewed as separate mechanisms, but rather part of a larger integrated model that combines threat assessment with processing of information from sensory systems to produce ongoing mobility.

Anxiety's effects on sensory integration during balance control

Many studies use virtual reality (VR), or visual illusions, paired with perturbations of a support base to study how vision and posture are linked and interact with each other. Jacob, Redfern, and Furman (Jacob, Redfern, & Furman, 1995) induced a sway response to optic flow stimuli in both people diagnosed with anxiety and SMD (space and motion discomfort, e.g. fear of heights) and non-anxious controls. Participants viewed a screen displaying optic flow stimuli through goggles that occluded one eye and only allowed central field vision in the non-occluded eye. The stimuli were a wall moving sinusoidally (towards or away from the viewer), a sinusoidally-moving tunnel, a constant tunnel, a checkerboard pattern that moved horizontally, or one that moved vertically. There were three baseline conditions: viewing a non-moving wall, viewing a blank stimulus, and eyes-closed, which were performed both before and after the optic flow conditions. Those with anxiety showed an overall greater sway response than the non-anxious controls but this

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difference was significantly greater in response to the optic flow stimuli, indicating a greater reliance on visual cues to control their balance. The authors argue that these effects tended to persist longer in anxious participants after the optic flow stimuli had ceased in the 'Eyes Closed' condition, based upon a trend towards significance in that condition. The authors claim that, taken together, their findings indicate that anxious individuals with SMD have an increased reliance on non-vestibular input (e.g. vision) compared to non-anxious individuals, which may be a candidate risk factor for developing acrophobia (phobia of heights). However, the study did not have a non-SMD anxiety group, which raises the possibility that the atypical vestibular-visual reliance weighting may be simply due to anxiety itself rather than SMD in particular. Furthermore, this study did not include a height manipulation, so it lacks the ability to shed light on whether height itself actually influences sway response through anxiety.

Similar results were found by Ohno, Wada, Saitoh, Sunaga, and Nagai (2004), who measured the correlation between the change in anxiety and body sway across two time points. Participants completed the State-Trait Anxiety Inventory (STAI; (Spielberger et al., 1979)) before being asked to stand on a platform while either keeping their gaze on a stable visual target (black circle on a white background), or while keeping their eyes closed. This was repeated a month later. Body sway was measured as a function of total length of body sway on the medio-lateral axis, antero-posterior axis, and the total length and enveloped area of sway. Analysis of the change in anxiety and the change in body sway parameters revealed that an increase in anxiety was positively correlated with an increase in antero-posterior sway as well as total enveloped area of body sway; however, these correlations were only significant in the Eyes Open condition. The authors suggest that these results demonstrate that anxiety has a specific effect on how visual information is processed in the brain in relation to postural control. Specifically, anxiety appears to solely influence the visual system in the context of orthostatic balance, since the effects were absent in the eyes closed condition. However, there is a possibility that participants became more anxious during the eyes closed condition, possibly leading to a difference in sensory reweighting. It is impossible to gauge from these results whether or not this is the case, since anxiety measures were only taken for each of the two sessions as a whole, rather than separately for each condition. Thus, while these results support the notion that anxiety produces a particularly strong effect on the processing of visual information, a more controlled paradigm is necessary in order to more closely scrutinise the relationship between increased anxiety and sensory reweighting.

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Inducing anxiety (postural threat) using height manipulations

In order to study the effects of state anxiety on balance maintenance, several groups of researchers have put younger healthy adults on a high platform as a way of eliciting perceived postural threat. This paradigm has often been successful in producing height-related anxiety in younger adults. For example, Adkin, Frank, Carpenter and Peysar (2002) tasked a group of young adults with a “rise-to-toes” activity while standing on either a low or a high platform, and either right at the edge or away from it. The magnitude of balance-controlling muscle activity during anticipatory postural control was reduced in the most threatening high-edge condition, which the authors argue demonstrates a conservative strategy to reduce destabilisation. In this condition, COP and COM data revealed that the participants shifted further backward away from the edge of the high platform, compared to the other conditions. These changes in postural control were also accompanied by an increase in stress levels, with increased threat (i.e., the high-edge condition) producing an increase in skin conductance and self-reported anxiety, and a decrease in confidence and perceived stability. Similar results were obtained by Naranjo, Allum, Inglis, and Carpenter (2015) who found that increased postural threat (standing at 3.2m height rather than ground level), and the associated increase in anxiety, produced elevated postural control responses in the form of increased vestibular evoked myogenic potentials (VEMPs) in the neck and lower leg muscles of young adults. Thus, it is possible to simulate postural threat in younger adults, and this method demonstrates how anxiety related to postural threat can have a potentially destabilising effect on balance control.

Cleworth, Chua, Inglis, and Carpenter (2016) examined how height anxiety affects bodily reactions to perceived height and support-base perturbations. Healthy young adults were exposed to a support base perturbation in a virtual reality (VR) environment whilst standing on either a “low” (0.4cm) or “high” (3.2m) narrow surface. Participants showed more COP displacement in reaction to support base perturbations in the high condition than when the virtual scene was at floor level (low condition). Additionally, this COP displacement occurred earlier at height than at ground level, which contrasts with Adkin and colleagues’ (2002) findings that height did not influence the timing of postural adjustments. Being at height also significantly increased balance-correcting tonic muscle activity in the arm muscles and lower leg muscles. Psychosocial responses such as balance confidence, fear, and anxiety were also measured, with balance confidence decreasing with height, and fear and anxiety increasing with height. The authors propose that participants’ postural reactions to the perturbation were potentiated by anxiety elicited by being up at a height.

Cleworth and Carpenter (2016) repeated their previous experiment, but with a real visual threat (as opposed to VR), and a stable base rather than a moving one. They examined participants’ awareness of postural sway by asking them to track how much they thought they were swaying in

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the antero-posterior plane using a hand-held potentiometer, while also measuring their actual postural sway amplitude and frequency. Participants displayed increased frequency and decreased amplitude of postural sway (i.e., stiffening behaviour) at height, and reported higher levels of anxiety, but indicated that they perceived that they were swaying just as much as at ground level. The authors suggest that sensory gain might be increased at height to compensate for stiffening, in order to maintain conscious perception of postural movement i.e., swaying (even though in reality they are not swaying as much). These results further support the concept that integration of different senses (i.e., visual vs. vestibular vs. proprioceptive) is affected by anxiety related to postural threat.

Vestibular Input Processing Changes as a Main Contributor to Anxiety-Related Postural Sway

While it is clear that anxiety has an effect on the integration of senses relevant to postural control, there exists a lot of dispute about whether or not balance responses to height-related anxiety are directly due to vestibular information processing changes. Many studies use electrical vestibular stimulation (EVS) to manipulate vestibular input during anxiety-inducing paradigms to measure vestibular contribution to postural control. This method works by placing electrodes (anode and cathode) on the mastoid processes, which deliver a small controlled electrical stimulation to the participant that affects vestibular input, eliciting a false sensation of body sway (Fitzpatrick & Day, 2004). There are several approaches to this method; galvanic vestibular stimulation (GVS) delivers a consistent current flow that evokes body sway toward either electrode, depending on the polarity of the stimulation (Inglis, Shupert, Hlavacka, & Horak, 1995; Welgampola, Ramsay, Gleeson, & Day, 2013). Stochastic vestibular stimulation (SVS) works in a similar fashion, but the signal is delivered in a random fashion, rather than consistently, which elicits greater signal-to-noise ratio, but does not offer as much temporal accuracy (Britton et al., 1993; Mackenzie & Reynolds, 2018; Nashner & Wolfson, 1974). Horslen, Dakin, Inglis, Blouin, and Carpenter (2014) propose that balance responses are directly due to vestibular gain increases from height anxiety, on the basis of finding that manipulating vestibular input using SVS had a greater effect on balance when applied at height compared to at ground level. These differences between surface height levels appeared at an early phase (<800ms following onset of SVS) as well as at a later phase (>800ms). Specifically, they argue that manipulating vestibular input at height (and therefore a higher level of anxiety) leads to a stronger correlation between vestibular input and the resulting balance reflexes compared to that at low surface level, as well as an increase in response gain.

Reynolds, Osler, Tersteeg, and Loram (2015) argue otherwise. These authors performed a similar experiment, using GVS rather than SVS. In contrast to Horslen et al. (2014) there was no

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difference in the 'early' response to vestibular stimulation between height and ground level, only in the 'late' response (an attenuation of sway). The authors propose that this was due to the CNS acting to reduce sway by utilising the proprioception feedback once it was available, rather than a direct effect of vestibular processing change on balance control. Reynolds and colleagues (2015) attribute this discrepancy partly to the use of SVS in Horslen and colleagues' (2014) study (as opposed to GVS), and argue that it does not sufficiently challenge balance. They also point out that the early balance responses recorded by Horslen et al. (2014) were mainly in the high frequency range, which are not typically thought to be directly indicative of conscious balance control (Dakin, Son, Inglis, & Blouin, 2007; Guerraz & Bronstein, 2008), so the relevance of these reported differences to balance is uncertain. Also, the analysis method used by Horslen et al. (2014) may have produced the difference in results; these authors used spectral analysis with SVS, which increases the statistical sensitivity to gain increases between the SVS and the balance response (measured in terms of ground reaction force). However, Reynolds et al. (2015) argue that this method is picking up small differences early on in the response, before proprioceptive information is integrated, that are irrelevant to balance control. Similar results were found by Reynolds (2010) when investigating effects of voluntary control of body sway while standing and being given SVS: early responses were no different between conditions (relaxed or trying to stand still), but late responses were different whereby consciously controlling movement caused attenuation of the late component, reducing response duration by 825ms, as well as less phase lag with SVS below 2Hz. This, they argue, demonstrates that the postural response evoked by vestibular stimulation is made up of two components: an early high-frequency response that occurs in proportion with background activity, and a later low-frequency component that is heavily influenced by conscious control of posture. This suggests that it is the later component that is relevant to cognitive influences on balance, such as increased anxiety.

Lim et al. (2017) used GVS to stimulate the vestibular system during quiet standing to examine how postural threat affects the coupling between the vestibular system and balance-relevant muscle responses. Rather than using raised height as a threat, the authors used the threat of a tilting platform, where the support surface was unstable, and participants were made to expect unpredictable mediolateral surface tilts. In the no threat condition, participants stood quietly on a stable surface. During trials, participants were blindfolded and instructed to lean forward slightly (to increase triceps surae activation). EMG was used to measure muscle activation. Their results indicated that anxiety (in this case, threat of perturbation) increases EVS-EMG coupling in leg and hip muscles through changes in cross-correlation, coherence, and gain in lower body muscles, providing further evidence that postural anxiety has a significant effect on vestibular-evoked responses. These

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results are consistent with studies that have used height as an anxiety-provoking manipulation, suggesting that these postural stiffening responses are a general vestibular response not specific to being on the edge of a high platform or to threat of movement alone.

It is evident from these studies that the vestibular system contributes to anxiety-related postural responses, though perhaps not directly. While it is clear that different sensory inputs are all contributing, further research with a more direct paradigm is necessary to parse these effects i.e., a method that is able to parse visual from non-visual (i.e., vestibular or proprioceptive) input. The VR postural threat paradigm has often been successful in producing height-related anxiety in younger adults (Cleworth et al., 2016; Cleworth & Carpenter, 2016; Cleworth et al., 2019), and the results help to give further insight into how FOF affects postural control. However, since older adults show age related changes in sensory weighting during balance control (Choy et al., 2003; Dumas & Krampe, 2010; Eikema et al., 2013; Ramkhalawansingh et al., 2018), it is arguable that older adults should be included as a comparison group when conducting research in this specific field. Once we know more detail about the mechanisms at play during postural threat in young adults, using a comparator OA group, it will be possible to evaluate whether or how these effects change with age. If research can elucidate how balance control is affected by anxiety and the physical and psychological effects of ageing, it may be possible to improve fall-prevention strategies by, for example, encouraging treatment to be focussed more on an individual's propensity towards anxiety, or their tendency to rely on one sense more than another. In short, findings from this type of study may lead to more specific and tailored interventions that cater to the varied and multi-factorial postural changes in at-risk populations.

Relevance to Neurodegenerative Disease

While so far, the relationship between anxiety and balance control has been discussed in the context of healthy populations, it is important to acknowledge how this relationship may change when observed in a clinical context. Parkinson's Disease (PD; characterised by primarily motor-related symptoms) is one such population in which balance control impairments are a key factor, and in which anxiety has been observed to have adverse effects. General anxiety is quite prevalent in PD – the lifetime prevalence has been reported at almost 50% (mostly Anxiety Disorder not otherwise specified; (Pontone et al., 2009)), and a recent systematic review puts point prevalence at 31% (Broen, Narayen, Kuijf, Dissanayaka, & Leentjens, 2016). While anxiety it is often thought to occur as a *result* of debilitating PD symptoms (Ellgring et al., 1990), many researchers also postulate that anxiety is a core symptom of PD (rather than a separate comorbid symptom) that may develop years before the PD is diagnosed (Shiba et al., 2000; Tolosa, Compta, & Gaig, 2007), perhaps due to

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the decreased dopaminergic transmission (Weisskopf, Chen, Schwarzschild, Kawachi, & Ascherio, 2003). As reviewed above, Balaban (2002) demonstrates the neural basis of this comorbidity, describing the neurophysiological links between areas that process anxiety and areas relative to balance control. In particular, PD patients with Freezing of Gait (FOG; see Chapter 4) seem to be affected particularly by anxiety in the context of eliciting and maintaining movement; Ehgoetz Martens, Ellard, and Almeida (2014) instructed patients with PD and FOG or without FOG to walk across either a low-threatening or a high-threatening environment in VR. PD patients with FOG reported higher levels of anxiety than patients without FOG and showed increased freezing episodes during the high-threatening condition compared to the low. While these results provide good evidence that anxiety is a key factor underlying this specific movement difficulty in PD, it remains unclear how this relationship works with regards to sensory reweighting. As stated above regarding healthy populations, it could be that increased anxiety affects sensory integration in the brain, and potentially increases reliance on visual information. In this specific subset of people with PD, effects of anxiety on postural control may be especially troublesome, and warrant further investigation in order to inform more effective therapeutic techniques for reducing the risk of balance loss and injury in this group.

These potential effects are compounded by a loss of functional proprioceptive processing (see Chapter 4). Since balance control requires adequate information from incoming sensory inputs in order to maintain balance (Butler et al., 2010; Della-Justina et al., 2015; Peterka, R. J., 2002), and that sensory inputs deemed as unreliable tend to be down-weighted (Bronstein, 2019), this arguably implies a need to rely on non-proprioceptive senses (e.g. vision) to a greater extent in people with PD than in healthy older adults. In other words, it is expected that those with impaired proprioceptive systems will rely more on visual input. Indeed, previous studies have suggested a heavier reliance on visual information for motor actions and balance in PD patients than healthy adults of a similar age (Azulay et al., 1999; Azulay, Mesure, Amblard, & Pouget, 2002; Cooke, Brown, & Brooks, 1978; Flowers, 1976; Vaugoyeau, Viel, Assaiante, Amblard, & Azulay, 2007), despite documented high-(Bowen, Hoehn, & Yahr, 1972; Davidsdottir, Cronin-Golomb, & Lee, 2005) and low-level (Bodis-Wollner et al., 1987; Price, Feldman, Adelberg, & Kayne, 1992; Silva et al., 2005) visual deficits (see Figure 2).

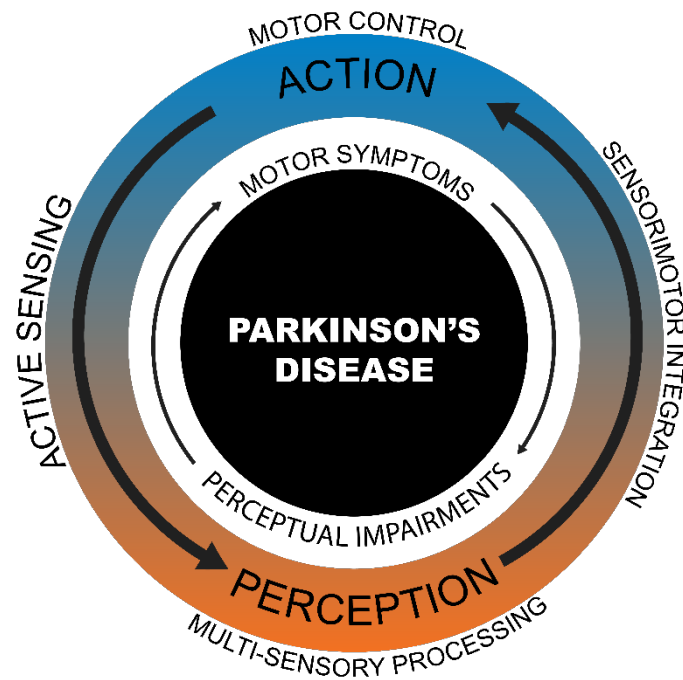


Figure 2. This version of the action-perception loop demonstrates how perceptual deficits, multisensory integration impairments, and motor symptoms may interact in Parkinson's Disease; adapted from Halperin et al. (2020).

Bronstein, Hood, Gresty, and Panagi (1990) demonstrate how people with PD are less able to suppress visually-evoked postural responses (VEPRs) following presentation of a visual perturbation incongruent with proprioceptive input, even after multiple trials. Bronstein et al. (1990) (1990) argue that this gives evidence for increased visual control of posture in PD patients, where visual dependency is not able to be suppressed despite evidence of the unreliability of this sensory input, potentially due to disease-related impairments in vestibulo-proprioceptive signalling. However, since manipulation of state anxiety was not included in this study, it remains unknown how increased state anxiety might influence PD patients' potential increased reliance on visual information for orthostatic balance compared to healthy cohorts. Following this rationale, and given the earlier discussed effects of posture-related anxiety on sensory reweighting, attempts to determine how sensory integration is affected by FOG severity and postural threat may help inform the direction to take when designing physiotherapeutic or behavioural strategies for those with PD and FOG, e.g. whether to focus therapeutic techniques on reducing anxiety related to posture. Since PD patients display a maladaptive reliance on vision, and are also heavily affected by anxiety, we could potentially improve balance control in this group by furthering the understanding of anxiety's role in visual reliance, i.e., if anxiety can be somewhat relieved in PD/FOG patient groups, this may help to ameliorate the hazardous effects of impaired sensory reweighting that might be exacerbated by anxiety.

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Conclusions & Introduction to Experimental Paradigm

Given the impact that anxiety appears to have on postural control in both healthy old and young populations as well as in clinical groups, it is arguably important to further elucidate how the relationship between anxiety and balance works – especially with regards to sensory integration. Evidently, further research is necessary to better understand the psychophysiological mechanisms behind balance control and fall risk under conditions of anxiety, so that more effective fall risk interventions might be developed. Specifically, questions remain over how anxiety influences the perception and processing (re-weighting) of incoming vestibular and visual information. One plausible explanation is that height-related anxiety is affecting the vestibular system gain and muscle spindle sensitivity in a way that increases perception of sway, therefore leading to increased stiffening of posture (Cleworth & Carpenter, 2016), and a subsequent shift to rely on another source of sensory information that is deemed more reliable. Research on people with Persistent Postural-Perceptual Dizziness (PPPD), a disease characterised by vertigo and perceived unsteadiness, suggests that anxiety is linked with PPPD, and also that one symptom of PPPD is an increased dependence on vision (Cousins et al., 2014a; Staab et al., 2017). This would suggest (though it is not explicitly demonstrated) that anxiety and visual dependence are linked, and that visual dependence can be exacerbated by unreliable signals coming from the vestibular system as a result of increased anxiety (Adkin & Carpenter, 2018; Popkirov, Staab, & Stone, 2018; Staab et al., 2017). Another possibility is that while postural-related anxiety leads to a gain in both visual and non-visual (i.e., vestibular/proprioceptive) input, the CNS still prioritises incoming visual information, leading to more reliance on vision than vestibular and somatosensory input. In other words, the increase in visual gain “shouts louder” than non-visual input and is therefore prioritised. These possibilities are not necessarily mutually exclusive, and research into this specific aspect of anxiety should aim to shed light on whether balance control changes in the context of anxiety are due to one, both, or neither of these.

Evidently, there are currently several gaps in knowledge of sensory reweighting under conditions of heightened postural threat: First, how anxiety affects sensory reweighting – *does* postural threat increase reliance on visual information? Secondly, does this change with age? Finally, are people with impairments in motor control and sensory integration, such as PD patients with FOG, more reliant on vision than healthy cohorts even under conditions of relatively low anxiety, and does this become compounded with postural threat?

The present set of experiments aimed to address these gaps in the research field by following a paradigm using virtual reality (VR) similar to Cleworth et al. (2016), but using an optic flow manipulation to alter visual information rather than manipulating proprioceptive information.

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The current studies use VR to provide a height-related threat (simulating postural anxiety) by placing participants either on a platform at the top of a cliff, or on the ground, while (in reality) standing on a force plate at ground level, and subjecting them to a visual perturbation. Broadly, this thesis attempts to explore how heightened postural threat affects balance control, and any further mechanisms that may underlie this relationship, in several different groups. Firstly, a small pilot study was conducted using young adults to optimise the overall protocol for the main experiments, specifically testing out some virtual environments and several visual perturbation sizes to determine the most effective virtual paradigm to use as a basis for the main experiments. Following this optimisation stage, an initial study was carried out on two healthy age groups (young and older adults) to investigate the effect of postural threat on postural reactions to the chosen visual perturbation i.e., to answer whether or not postural threat (i.e., anxiety) leads to an increased reliance on vision, and whether this effect would change as a function of age. Following these results, the second study used the same paradigm as Study 1 in a clinical subgroup of Parkinson's Disease patients who reported regularly experiencing FOG, with the aim of improving knowledge about how people with increased need for reliance on vision reweight their reliance on different senses following a disparity, and how postural threat affects this. Finally, the third study focused on young adults and set to further delve into the relationship between postural anxiety and response to discrepant visual information by including other factors, namely direction of attention (i.e., internal/increased conscious motor control vs. baseline), into the original paradigm.

Chapter 2. Methodology & Protocol Optimisation

Part 1. Description of building a virtual environment using Unity 3D, and the coding/design of the visual perturbations paired with a sound cue for synchronisation

One of the possible ways that postural threat affects balance control, as discussed in the previous chapter, is by affecting the integration of various sensory inputs (Cleworth et al., 2016; Cleworth & Carpenter, 2016; Cleworth et al., 2019; Naranjo et al., 2015; Paterson & Huxley, 2011; Sturnieks, Delbaere, Brodie, & Lord, 2016). For example, Cleworth and Carpenter (2016) demonstrate that people who are placed at height show a reduced amplitude of postural sway, despite perceiving themselves to be swaying at similar amplitudes to when standing at ground level. This finding indicates that postural threat may alter the integration of sensory inputs (Horslen & Carpenter, 2011; Horslen, Dakin, Inglis, Blouin, & Carpenter, 2015). Notably, results from other studies provide examples of how anxiety influences sensory function, and infer that anxiety is associated with an increase in reliance on visual information to control balance (Schniepp et al., 2014; Willey & Jackson, 2014); however, the nature of this relationship remains unclear.

In preparation for empirical studies, we aimed to create an environment to test the effects of postural threat on balance control while also prioritising participant safety. This necessitated a method that offered both a means to induce postural threat as well as to introduce sensory disparity. While previous experiments examining the effects of height-related anxiety on balance control have used real platforms to induce postural threat (Adkin et al., 2002; Cleworth, Horslen, & Carpenter, 2012; Cleworth & Carpenter, 2016; Naranjo et al., 2015), it is difficult to achieve this, combined with causing sensory incongruency, in a physically safe manner. To this end, it was decided that a virtual environment should be used, paired with the HTC Vive virtual reality (VR) system that uses a head-mounted display (HMD). Following the described work of previous researchers examining the effects of postural threat on balance control, it was decided that the most effective manipulation of postural threat to induce anxiety would be to include a condition where participants were situated at the edge of a platform at a large height in VR. To isolate visual input and introduce sensory disparity, a visual perturbation was determined to be the most effective method. A visual perturbation can be created by rotating the visual scene within the HMD, creating the illusory sensation that one is moving, while the non-visual sensory inputs are delivering contradictory signals (i.e., of not moving).

In order to optimise the virtual paradigm, a pilot study was conducted using several different perturbation magnitudes, along with measurement of anterior-posterior Centre of Pressure (COP) displacement and verbally-reported state anxiety changes. This chapter describes this process.

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Aims

The present pilot experiment aimed to optimise the perturbation and threat manipulation characteristics of the subsequent empirical studies. The intended outcome was to determine which manipulations would best serve as a means to measure how reliance on visual vs. non-visual input changes with anxiety. Specifically, the pilot study aimed to answer two questions: 1) would our manipulation of postural threat be successful in producing an increase in anxiety and changes in postural response, and 2) what kind of visual perturbation would be the most effective as a manipulation of isolated visual stimulation in a postural threat paradigm. The results of this pilot study would be used to help shape the methodology for further empirical work detailed in Chapters 3-6.

Materials & Methods

Participants

10 young adults (7 males), aged 23-28 years old ($\mu = 25.6$; $s.d. = 2.32$), were recruited through Brunel University London. No participants reported any diagnosed musculoskeletal or neurological disorders. All participants provided written informed consent.

Equipment

Anxiety Manipulation

To manipulate anxiety (particularly anxiety related to postural threat), two virtual environments were created – one with a postural threat and one without. These environments were created using Unity 3D (version 5.5; Unity Technologies, 2015). One of the environments consisted of a wooden platform (similar to a diving board) atop a cliff overlooking a long gully (to induce anxiety), with some trees dotted around the top of the cliff where the participants were “standing”, and at the bottom of the gully, to provide some visual reference and easier distance perception. This was the “Threat” condition. The other environment was similar in every way except for everything being at ground level, as opposed to standing at height; this was the “Ground” condition. A virtual camera was placed in the scene. In the “Threat” condition, this was placed on the edge of the virtual wooden platform, overlooking the gully. In the “Ground” condition, it faced the same direction but at ground level. The perspective from this virtual camera was then displayed through the HMD, allowing the participants to perceive themselves as being either standing on the edge of the cliff, or at ground level (see Figure 3).

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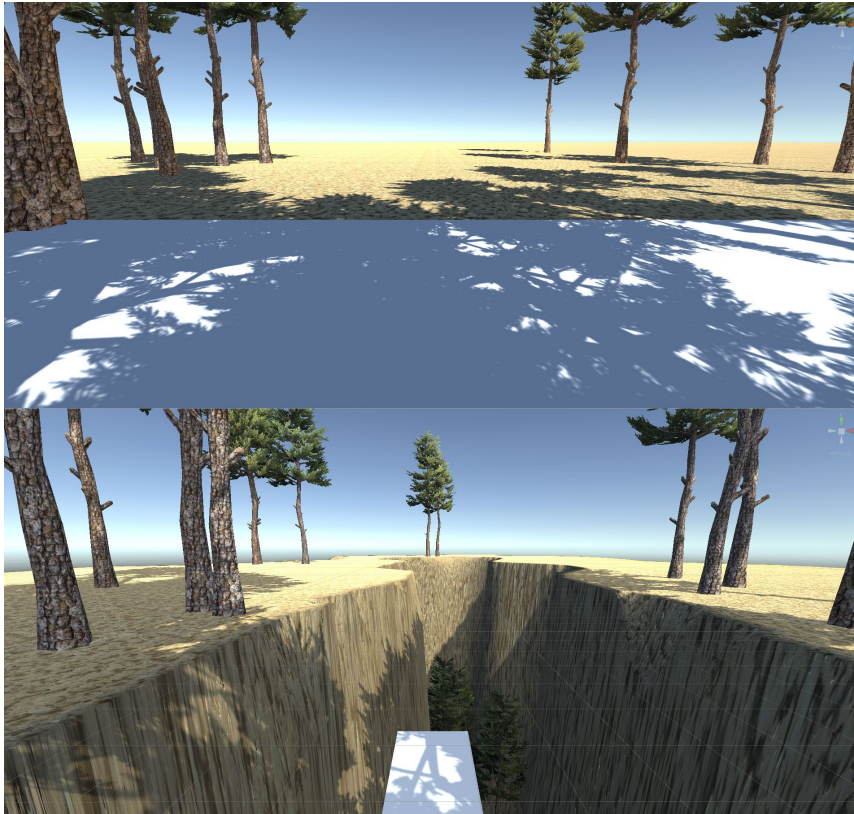


Figure 3. First Person View of the virtual “Threat” (top) and “Ground” (bottom) conditions; grey model represents position of participant in VR.

VR System

The VR system was calibrated so that the platform in VR corresponded to the force platform in reality; this allowed participants to perceive themselves as being the correct height up from the ground once the HMD was fitted i.e., the visual information was representative of that perspective in VR. The HMD system used to display the virtual reality was the HTC Vive (1080x1200 per eye resolution, 90Hz refresh rate, 110 degrees Field of View [FoV]). Using an HMD denies the full availability of visual information in the periphery, thereby restricting optic flow information important for postural control (Piponnier, Hanssens, & Faubert, 2009). This inherently compromises the potency of the visual perturbations delivered. Nevertheless, the FoV afforded by recent VR headsets such as the HTC Vive or Oculus Rift appear to be sufficient in providing sufficient peripheral input to stimulate the visual field and specify some degree of self-motion. For example, Dennison and D’Zmura (2018) presented visual perturbations to participants via both a monitor and an HMD (Oculus Rift), and found that participants demonstrated increased postural sway when the perturbation was presented through the HMD than from a monitor. While the monitor they used permitted a smaller FoV than the HMD, this nevertheless provides evidence that using an HMD provides sufficient peripheral input. Despite it being unclear whether it is the size of the FoV or the

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immersion of the VR that affords a larger postural sway, it seems that a VR HMD is a viable and flexible option for providing sensory stimulation in an empirical context.

Many postural control studies use a CAVE system to present their virtual environments (Greffou et al., 2012; Keshner & Kenyon, 2000; Slaboda, Lauer, & Keshner, 2011), which is a room-sized 3D video and audio environment where participants are surrounded by four projection screens for the walls and floor. Participants are required to wear stereoscopic glasses which restrict the FoV to 100 degrees – a smaller FoV than that afforded by the HTC Vive, and still sufficient in producing postural responses to virtual moving fields. Furthermore, a clear advantage of using an HMD (as opposed to a CAVE system) is that it enhances the immersion and permits the interaction of the participant with proximal environmental features.

Visual Perturbations

To explore the specific effects of different visual sway magnitudes, the experiment elicited three different visual perturbation sizes, with an aim to determine which perturbation type would be most effective for measuring visual reliance in a postural threat paradigm. Wang, Kenyon, and Keshner (2010) used a similar method and found that increasing the velocity of optic flow in the pitch-up (i.e., nose-upwards) direction significantly affected both Centre of Mass (COM) and ankle angular displacements (see previous chapter). This observation led us to expect that a larger/faster perturbation would produce a postural response of greater magnitude than a smaller/slower perturbation.

Three visual perturbations in the anterior-posterior (AP) direction were delivered to participants, in both the Ground and Threat conditions. The order of threat condition and perturbation size was counterbalanced for each participant. These perturbations lasted for two seconds, and consisted of a sinusoidal movement in the pitch-up (posterior) direction for the first 1000ms, followed by an pitch-down (anterior) motion back to upright over the latter 1000ms. The perturbation sizes were ‘large’ (15° per second), ‘medium’ (10° per second), or ‘small’ (5° per second). In Unity3D, these values represent Euler Angles. By attaching a code to the perturbation animations in Unity, each of the perturbations could be called with an individual keypress by the experimenter. In order for the perturbations to occur in a way that made the visual scene move in a way concurrent with the experience of swaying in the posterior direction, the HMD was made a “child object” of a 3D figure “parent” object in Unity. The animations were attached to this parent

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object. Anything that occurred with the parent object, occurred in the child object i.e., the view from the HMD¹.

Technical Specifications

Unity 3D and the HTC Vive system were run through a Viglen Genie desktop computer (Dell Precision Tower 3620, i7-6700 processor, GeForce GTX 1080 Graphics Card; Windows 10). The COP data were collected through Vicon Nexus 2.5 on a Dell Precision Tower 5810 (Windows 10).

Kinetic data were recorded using a Kistler Forceplate (600x400x35mm, Kistler model 9286, SN1426829, software Nexus 2.5, Amp Control Unit Kistler 5233A), with feet positioned on the centre of the forceplate in a natural relaxed stance. COP data were collected from the forceplate through 8 channels measuring ground reaction forces and sampled at 1000Hz. These data were synchronised with the sway animations using a sound cue that was triggered by the start of each animation in Unity3D and fed into the channel amplifier that received forceplate input, using a single separate channel.

To ensure participants' safety during the experiment, they were secured in a fall-arrest harness attached to a scaffold frame throughout the experiment to prevent falling and injury.

Procedure

All participants received a participant information sheet briefly describing the aims, procedure, and any associated risks, along with a consent form to sign. The participants were made aware that they were able to leave at any point during the experiment with no adverse consequences. Following informed consent, participants were strapped into the safety harness, and the HMD was secured and adjusted to a comfortable position on the head. Once the HMD was activated, participants experienced themselves as standing on the white platform either in the Ground environment or the Threat environment. Participants walked one meter up to, and then stood on, the forceplate, which corresponded to the edge of the white platform in Threat, and the central area of platform in Ground. Following a key press by the experimenter, the participants experienced one of three pitch-up rotations to mimic the experience of balance loss i.e., the visual scene rotated in the pitch-up direction, and then in the pitch-down direction, returning to upright position, in virtual reality.

¹ At the time the data was collected, it was not possible to directly animate the VR system, therefore any animations had to be attached to a "parent" object which would consequently cause animations to occur in the VR headset. As of 2020 it is now possible to directly animate a VR system in Unity 3D.

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During each threat level condition, participants experienced three perturbations (one of each size), with a randomised number of between 2 and 5 seconds' break between each perturbation. The order of the visual perturbation sizes was counterbalanced for each participant to prevent order effects of habituation.

Following each trial, participants were given the Mental Readiness Form (MRF) questionnaire to measure state anxiety (Krane, 1994). The MRF uses three questions regarding feelings of worry (cognitive anxiety), body tension (somatic anxiety), and confidence, scored on a scale of 1 to 11². After experiencing each of the three visual perturbations in both conditions, the session finished. Participants were then free to remove the HMD and received a full debrief.

Analysis

The postural reaction to the perturbation was captured by selecting the data from the perturbation onset (identified via the sound cue) to three seconds following perturbation onset. The data from these sections were filtered in MATLAB (second order low-pass Butterworth filter with a cut-off frequency of 5Hz; R2017a, The Mathworks, Inc.), and the Root Mean Square and Range of COP displacement were calculated for this three-second perturbation period. Therefore, the following variables were calculated for each participant: the Range of COP Displacement (RCD) and RMS of COP Displacement (RmsCD) during the perturbation, for each of the three perturbation sizes.

RmsCD was non-normally distributed for the Threat trials where a large perturbation was used, so a Related-Samples Wilcoxon Signed Rank test was used to test for differences between perturbation sizes. RCD was non-normally distributed for the Threat trials where the large and small perturbations were used, so a Related-Samples Wilcoxon Signed Rank test was used to test for differences between perturbation sizes.

MRF data were normally distributed for the Threat condition, but not for the Ground condition, therefore a Wilcoxon Signed Rank test was used to test for differences in self-reported state anxiety levels between conditions.

Results

At Ground, the RCD response to the large perturbation was significantly larger than the response to the small perturbation ($p = 0.013$, $Z = 2.497$, $r = 0.789$). The medium perturbation did not elicit responses of significantly different magnitude to either the large ($p = 0.333$, $Z = 0.968$, $r =$

² NB since a higher score in the confidence question denotes lower anxiety, the confidence subscale was reverse coded.

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0.306) or small ($p = 0.059$, $Z = 1.886$, $r = 0.596$) perturbations. At Threat, however, there was no longer any difference between the RCD responses to large and small perturbations ($p = 0.169$, $Z = 1.376$, $r = 0.435$), with the only significant difference occurring between the large and medium perturbations ($p = 0.028$, $Z = 2.191$, $r = 0.693$). This pattern of results was also observed for the RmsCD responses, with a significant difference observed between the small and large perturbations at Ground ($p = 0.037$, $Z = 2.09$, $r = 0.661$) but not at Threat ($p = 0.508$, $Z = 0.663$, $r = 0.209$; see Table 1 and Table 2). Analysis on the MRF data found that participants' self-reported state anxiety was significantly higher at Threat ($\mu = 13.63$) compared to Ground ($\mu = 5.38$; $p = .007$, $Z = 2.675$, $r = 0.892$).

Table 1. Means and standard deviations of range of anterior-posterior COP displacement (RCD) at Ground and Threat using three different perturbation sizes. Square brackets denote significant difference between two variables ($\alpha=0.05$).

RCD	Ground μ (s.d.) (mm)	Threat μ (s.d.) (mm)
Large	16.99 (12.33)	27.81 (23.76)
Medium	12.75 (6.37)	14.81 (6.38)
Small	8.93 (4.69)	18.13 (14.22)

Table 2. Means and standard deviations of RMS of anterior-posterior COP displacement (RmsCD) at Ground and Threat using three different perturbation sizes. Square brackets denote significant difference between two variables ($\alpha=0.05$).

RmsCD	Ground μ (s.d.) (mm)	Threat μ (s.d.) (mm)
Large	6.71 (4.06)	9.76 (7.36)
Medium	5.89 (3.69)	6.46 (2.98)
Small	3.29 (1.83)	7.84 (5.44)

Brief Discussion

This pilot study aimed to explore the efficacy of a VR postural threat environment in inducing anxiety, and what the ideal characteristics are for a visual perturbation to be effective in measuring visual reliance in a postural threat context.

First, the healthy young adults in this pilot study reported significantly higher anxiety levels in the Threat condition compared to the Ground condition, indicating that the environment designed for this paradigm was successful in inducing anxiety in the form of postural threat.

Secondly, given that the smallest perturbation elicited a change in COP displacement from Ground to Threat and elicited a postural response of comparable size to the large perturbation, it seems that a smaller sensory discrepancy is a more useful manipulation to use for measuring the effects of postural threat on visual reliance in sensory reweighting. While the larger perturbations do produce a larger postural response than the small perturbation at Ground, there is no difference between the small and large perturbation responses at Threat. Therefore, there is a possibility that a ceiling effect occurs when participants experience a larger disparity between visual and non-visual sensory input, where the capacity for change in postural response with a psychological manipulation such as induced anxiety is curbed by the size of the disparity at baseline. In order to minimise the risk of a ceiling effect occurring, it appears that a more subtle perturbation would be more useful to help answer the research question(s) of how postural threat affects visual reliance for postural control.

In sum, these findings suggest that a) the threatening condition we designed was successful in increasing anxiety, and b) that the most useful perturbation size to use for this paradigm appears to be the smaller one.

Part 2: Next steps*Optimisations*

Given the results of this pilot study, the smallest perturbation (5° per second) was chosen for all subsequent experiments using this paradigm. After each participant session, participants were asked about their thoughts on the environment and how it might be improved in terms of immersion. Following feedback from these participants, more objects were added to the virtual environment to improve the sense of distance accuracy. Specifically, objects closer to human size (such as barrels and a cart) were added to both conditions (see Figure 4). The objects were positioned at the same orientation and distance from the participant in each condition. A fixation point (red asterisk) was also added at roughly eye level to each condition (and kept consistent between conditions) to maintain consistency of fixation direction across conditions and participants.

Furthermore, several studies in the field have observed habituation to the presentation of repeated incongruent sensory signals, manifested in a reduction in postural reaction to repeated perturbations (Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol, Runtz, & Pai, 2004). Bronstein (1986) found that participants' visually-evoked postural responses (VEPRs) to an incongruent visual stimulus was significantly lessened after one presentation, and argued that if an unreliable sensory signal is repeatedly presented, the central nervous system (CNS) soon recognises the input as false, and begins to downweight any sensory information arriving via this input. Therefore, in order to avoid any habituation effects that might occur with multiple or continuous perturbations, we limited the incongruent visual perturbation to a single instance per trial for the three main empirical studies.

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Figure 4. First-Person view of improved VR environment for Threat (Top) and Ground (Bottom) conditions

Changes to Main Outcome Measures

Once interpretation began on the empirical data following the pilot, some issues became clear. One concern with using peak-to-peak Range of AP COP displacement as the primary outcome variable is that it does not account for factors, other than visual reliance, that may influence the overall range of movement, especially around the posterior peak. The use of a perturbation that reverses and moves in the pitch-down direction again following the first 1000ms of pitch-up motion, while designed to be broadly representative of a momentary loss of balance, prevents analysis of postural behaviour in the latter half of the perturbation period. This is because it is difficult to know whether the subsequent postural behaviour following reversal of the perturbation is influenced by attempts to return to upright standing, or continued visual influence of the perturbation. Therefore, examining the Range of COP displacement over the whole 2000ms perturbation period is problematic. In previous research observing postural response to visual perturbations (Keshner & Slaboda, 2009), stimulating optic flow in one direction initially produces a corrective response in the opposite direction. Therefore, we felt it necessary to reconfigure our interpretation of people's postural responses and what the main outcome measures should be.

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Based on existing work within this research area (particularly the work of Keshner and Slaboda (2009)), we decided that the most informative behaviour to look for in this context is the initial postural movement that counteracts the direction of a visual perturbation (for example, an anterior postural response to a visual stimulation that gives the participant the impression that they are swaying in the pitch-up/posterior direction). Thus, the main outcome of this reconfiguration of analysis was that participants' anterior peak (relative to their baseline position) during the first 1000ms following the initial pitch-up movement of the visual perturbation (i.e., Relative AP) became our primary outcome measure: the primary postural response to the pitch-up visual perturbation. The reversal motion of the perturbation was preserved, despite no longer measuring responses during this part of the perturbation, since it also serves the purpose of minimising the potential for habituation to the perturbation. That is, since it returns the participant's view to upright, consistent with non-visual sensory information, there is less chance of visual information being downweighted before the next trial starts which would have confounded postural response observations of the subsequent trial. This also reinforces the rationale for selecting the smallest perturbation, since a more subtle perturbation helps to minimise the risk of habituation to the incongruent visual disturbance compared to a larger one.

We also explored the possibility of further classifying participants' responses, such as early vs. late response, as other studies have done (Haas, Diener, Bacher, & Dichgans, 1986). However, the perturbation is unlike other visual perturbations previously used in the field in terms of speed – the perturbation was, on average, six times slower than the perturbation speed used in studies such as that of Keshner and Slaboda (2009), thus with a flatter acceleration of the perturbation trace. This also impaired the feasibility to accurately discern the moment at which participants became aware of the perturbation, thus it was not possible to categorise people's responses into subgroups. Therefore, we took the anterior peak occurring between perturbation onset and the point at which the perturbation reversed its movement again as the participant's primary response. While use of a slower, small perturbation may bring an inevitable delay in response, the observations from this initial pilot study suggest that it is important to use a compelling perturbation where sensory discrepancy is harder to detect, in order to more accurately isolate the effects of postural threat on visual reliance.

To further investigate the spatiotemporal nature of participants' postural response, we also measured velocity i.e., the speed of initial movement between perturbation onset and when participants reached their anterior peak. Thirdly, we measured the time taken to reach the anterior peak (AP Latency) as a measure of response time to the perturbation. These additional measures allow for more detailed comparison of postural responses between conditions or subject groups,

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where, for instance, the amplitude of the response is comparable but differences in latency may indicate meaningful effects. Lastly, Carpenter and Adkin (2018) have argued that using time windows of less than sixty seconds results in unreliable measures of RMS. Therefore, in the following empirical studies, RMS was not calculated for the perturbation period (which only lasts 2 seconds).

Regarding sample size, a G*Power analysis on the difference in RCD between Ground and Threat in reaction to the small perturbation at $1-\beta = 0.95$ revealed a desired sample size of 24 participants (Faul, Erdfelder, Lang, & Buchner, 2007). However, since the planned outcome measures now only focus on a specific part of the whole range of anterior-posterior postural sway during the perturbation, and given the inherent data variability due to using only a single trial per condition, we aimed for a slightly larger sample size of 30 for each group to ensure sufficient power.

These optimisations were implemented for the following empirical studies, all of which used the described paradigm. The first study compared young and older adults' postural responses to the visual perturbation at both Ground and Threat to explore the effects of increased state anxiety and age on visual reliance. A second study explored the effects of these factors in people with Parkinson's Disease with Freezing of Gait (when compared to healthy older adults) to explore how this neurodegenerative disease may impact the relationship between anxiety, age, and visual reliance. A final study assessed a group of younger adults and repeated the same paradigm with the additional independent variable of level of internal focus, in an effort to elucidate how increased conscious control of movement may further alter reliance on visual input when controlling balance.

Chapter 3.

Study 1: Increased Perception of Postural Threat Increases Reliance on Vision to Control Balance in Young and Older Adults

As described in Chapter 1, to maintain balance the Central Nervous System (CNS) must integrate information from different sensory systems, such as vision, vestibular input, and proprioception in order to regulate patterns of muscle activation (Della-Justina et al., 2015; Peterka, R. J., 2002). This can be demonstrated by paradigms that manipulate self-motion perception (e.g., heading estimates). In isolation, unimodal presentation of information (e.g., visual cues alone) allows some estimation of self-motion. However, when separate and congruent sensory cues are presented together, estimates become more accurate (Butler et al., 2010; Butler et al., 2011; Campos & Bühlhoff, 2012). This is known as the redundancy phenomenon, whereby observers integrate several estimates that are weighted according to their respective 'perceived' reliability and yield more accurate estimates of self-motion than they would from one estimate alone (Butler et al., 2011; Fetsch et al., 2009).

To study the intricacies of the different sensory inputs' contribution to balance control, many researchers have designed paradigms that isolate individual sensory inputs, for example using visual perturbations that create optic flow in the relative absence of change in vestibular or proprioceptive input (Lee, D. N. & Lishman, 1975). However, since this often involves presenting information to one sense that is incongruent with others, one must account for the possibility of participants habituating to the perturbation if it is presented multiple times. Bronstein (1986) demonstrated a significant decrease in postural response to a repeated incongruent visual perturbation and argued that following the initial perturbation, since the visual signal is deemed to be unreliable, the CNS reweighted sensory inputs to be more dependent on non-visual information. Other research supports the notion that repeated or prolonged exposure to incongruent sensory information results in a progressive sensory reweighting that may not accurately reflect participants' initial weighting (Bronstein, 2019; Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol et al., 2004).

Virtual reality (VR) is a useful tool for parsing different inputs to study sensory reweighting. Keshner and Slaboda (2009) used discrete perturbations in VR to examine sensory reweighting in young adults (YAs), older adults (OAs), and post-stroke patients. Participants stood on a platform that tilted backwards 3° into a position of dorsiflexion at a speed of 30°/s and remained stable at this 3° tilt for 30s, before slowly tilting 3° forward again, returning to the starting level position at a speed of 0.1°/s. Meanwhile, the visual surroundings either i) moved to match the motion of the head (i.e., congruent with a natural visual response to the physical perturbation), ii) moved in a

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pitch-up motion (i.e., incongruent with the physical perturbation, giving a visual perception of tilting forwards) at varying speeds, or iii) obscured (i.e., participants were in the dark). EMG and Centre of Mass (COM) responses were measured. In all groups, the postural responses to the tilting support base was affected by the presence of incongruent visual field motion. For example, participants showed greater lower limb muscle RMS values during visual field motion than when vision was absent. These results suggest that visual stimulation has a considerable effect upon postural control, indicating an increased reliance on vision given an unstable base of support.

One notable finding of Keshner and Slaboda (2009) is the nature of the COM response to the physical dorsiflexion perturbations. Participants first displayed an initial anterior movement to counteract the posterior perturbation, followed by an accommodating posterior sway response, which (particularly in OAs) was increased when the visual field movement conflicted with the physical perturbation, and often overshot the original COM position. Thus, it appears that the initial response to optic flow in one direction is a postural response in the opposite direction, and that this provides a useful measurement for gauging the relative reliance on visual information during experiments investigating sensory reweighting during optic flow.

Ageing & Postural Sensory Processing

The efficiency of many biological processes declines with age, and multisensory integration is no exception. Studies using unimodal vs. bi/multimodal cue conditions find that OAs benefit more from multiple cues than do YAs (Peiffer, Mozolic, Hugenschmidt, & Laurienti, 2007); however, these studies often also find that this integration is slower and less efficient in OAs than YAs (Diederich, A. et al., 2008; Mozolic, Hugenschmidt, Peiffer, & Laurienti, 2012; Ramkhalawansingh et al., 2016). Furthermore, while YAs demonstrate an ability to combine cues flexibly, OAs show deficits in integrating cues in an effective manner, especially when one or more cues are incongruent. For example, OAs demonstrate less ability than YAs to maintain a straight course towards a visual target when discrepant vestibular information is introduced (Deshpande & Patla, 2007). These sensory integration deficits have been implicated as a primary underlying mechanism in the reduced ability to maintain stability both while standing and walking compared to YAs (Hausdorff et al., 2001; Horak et al., 1989). The research community widely acknowledge age-related increases in visual reliance, evidenced primarily through decreased stability when asked to maintain balance with eyes closed (Choy et al., 2003) or higher visual field dependence scores on rotating visual field tests (Agathos et al., 2015). Isableu, Ohlmann, Crémieux, and Amblard (2003; 2011) expanded on this work and argued that a persistent and consistent upweighting of visual information is associated with impaired ability to dynamically reweight multiple sensory inputs during sensory disturbance. Eikema,

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Hatzitaki, Konstantakos, and Papaxanthis (2013) suggest several reasons for this impairment; lower weighting on proprioception caused by rigid dependence on visual input could hamper older adults' ability to detect a change in accuracy of incoming proprioceptive input, therefore impairing the ability to ignore inaccurate information. For example, in a study using a graduated tuning fork to stimulate the ankles with vibrations of varying amplitudes, OAs with lower gait and balance abilities demonstrated reduced sensitivity to this stimulation (Buchman, Wilson, Leurgans, & Bennett, 2009), indicating a relationship between proprioceptive integration deficits and balance control. Prioritisation differences observed in sensory reweighting could also be due to deficits in attentional set shifting, which could negatively affect the ability to shift sensory reliance from an unreliable input to an appropriate accurate source, and have been demonstrated to correlate with balance impairment (Eikema et al., 2013; Hawkes et al., 2012). Another potential culprit is a decline in cognitive motor abilities such as movement prediction and planning (Skoura et al., 2008).

In the aforementioned study by Keshner and Slaboda (2009) using a discrete visual perturbation in VR paired with a support-surface perturbation, older adults and post-stroke patients were especially sensitive to the visual field motion compared to young adults, providing further evidence for age-related increases in visual reliance (Agathos et al., 2015; Choy et al., 2003). A subsequent study observed YAs and OAs using a similar paradigm, but with a continuous rotating visual field, and showed that OAs exhibit larger Centre of Mass (COM) and Centre of Pressure (COP) responses in the (anterior) direction of the visual field motion, as well as increased visual reliance in standalone Rod and Frame tests. The authors suggested that OAs tend to show more stiffening actions (such as increased muscle co-contraction in the ankle and less muscle modulation) as well as heightened visual sensitivity, which impairs their ability to maintain postural control during perturbations and incongruent sensory information (Slaboda et al., 2011).

These studies have made valuable contributions to our understanding of how sensory integration is affected by increased age, but due to methodological limitations, the question of how ageing affects reweighting of sensory inputs (particularly visual vs. non-visual) is yet to be directly evaluated. For example, while Choy et al. (2003) report an augmented reliance on vision due to increased age, their approach to quantifying postural sway, after instructing participants to close their eyes, represents an indirect measure of visual reliance. As such, this method does not account for the possibility that participants could dynamically reweight sources of sensory information within a given trial to accommodate the absence of visual information, and consequently adopt an altered postural strategy. For example, the increased instability observed in OAs during eyes-closed conditions could either be due to an inability to reweight sensory information, or it might suggest that OAs have deficits in non-visual sensory systems that result in balance problems when they try to

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rely on these non-visual systems in situations where vision is unavailable. Furthermore, while informative, the use of rotating visual surrounds in many studies, to demonstrate persistent reliance on vision (Agathos et al., 2015; Lord & Webster, 1990; Redfern & Furman, 1994), is somewhat restrictive. While these findings indicate an inability to down-regulate visual reliance, the intra-sensory disparity (e.g. illusion of self-motion) is often presented continuously, and therefore unable to necessarily indicate the level of reliance in contexts where participants are unaware that the visual information is incongruent (i.e., untrustworthy; (Bronstein, 2019; Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol et al., 2004)).

Thus, it is not clear how increased age leads to differences in sensory reweighting, but the cognitive/attentional factors are one hypothesised explanation. Another possibility is the observation that conscious control can influence vestibular responses (Reynolds, 2010). Conscious control of movement is a common theme in older adult research, and is often found to be elevated in adults who have increased concerns about their movement – particularly with regards to falling (Boisgontier et al., 2013; Chow, Ellmers, Young, Mak, & Wong, 2018; Clark, 2015; Ellmers, Cocks, & Young, 2019b; Magnard et al., 2019; Uiga et al., 2018; Wong, Masters, Maxwell, & Abernethy, 2008; Young & Williams, 2015). Age-related concern about falling may be the basis for how anxiety can influence sensory reweighting and other associated behaviours that may influence fall risk. In Older Adults (OAs), the effect of perceived postural threat on balance control is a particular concern, since anxiety about falling is apparent in between 12% and 85% of OAs (Legters, 2002; Scheffer, Schuurmans, Van Dijk, Van Der Hooft, & De Rooij, 2008) and is strongly associated with an increased likelihood of falling (Hadjistavropoulos et al., 2011).

Effects of Anxiety on Postural Control

Previous work has shown that anxiety, such as that induced by perceived threat to balance, may influence the way sensory inputs are integrated to control posture (Ohno et al., 2004). For example, Balaban (2002) described connections between areas of the brain that process and regulate anxiety and balance-relevant sensory information, such as between the limbic system and parabrachial nucleus. In terms of behavioural observations, Jacob, Redfern, and Furman (2008) induced a sway response using optic flow stimuli in anxious patients with space-motion disorder (SMD) and non-anxious controls. The anxious participants displayed greater reliance on non-vestibular input (e.g. vision and proprioception) than non-anxious individuals. This raises the question whether such atypical vestibular-visual reliance might be partially due to anxiety-related factors; however, many of the previously mentioned studies examining age-related sensory integration differences did not include a manipulation of, or control for, levels of anxiety (Choy et al.,

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2003; Keshner & Slaboda, 2009; Slaboda et al., 2011), therefore it remains unknown exactly how anxiety affects sensory reweighting under conditions of congruent or incongruent visual and non-visual information.

The manipulation of anxiety in postural control studies has typically involved raising people up at height on a platform to increase perceived postural threat (Adkin & Carpenter, 2018). Cleworth, Chua, Inglis, and Carpenter (2016) placed young adults on a raised virtual platform while recording kinetic, kinematic, electromyographical, and emotional responses, and subjected them to unpredictable anterior and posterior support-surface perturbations. Participants displayed increased fear and anxiety, concurrent with increased muscle activity in the tibialis anterior prior to the perturbations. In response to the perturbations, participants produced increased mean lower leg and arm muscle activity, as well as earlier and larger Centre of Pressure (COP) displacements at virtual height compared to ground level. Supported by several previous studies (Cleworth & Carpenter, 2016; Cleworth et al., 2019; Lim et al., 2017; Phanthanourak, Cleworth, Adkin, Carpenter, & Tokuno, 2016), these results suggest that postural threat induces increased sensory gain as well as increases in EMG and sway frequency, indicative of a 'conservative stiffening strategy' (Carpenter, M. G., Frank, Adkin, Paton, & Allum, 2004; Cleworth et al., 2016). In the presence of the perturbation, the authors argue that the observed earlier and larger postural responses are due to threat-induced sensory gain and stiffness (Cleworth et al., 2016; Sinha, 1995). There are several studies that indicate a role of anxiety in increasing vestibular gain (Lim et al., 2017; Naranjo et al., 2015). Similarly, previous findings have also implicated anxiety as having an augmenting effect on muscle spindle sensitivity (Horslen, Murnaghan, Inglis, Chua, & Carpenter, 2013).

Aims & Hypotheses

Overall, there appears to be a pervasive role of anxiety in affecting sensory integration across sensory modalities. However, the specific impact of anxiety on visual reliance is less clear. It is evident that further work is needed in order to better understand the influence of anxiety on balance-related sensory integration. The main aim of the current study was to evaluate the influence of increased perception of postural threat (and corresponding increased anxiety) on responses to a visual perturbation in both young and older adults.

The current study used VR to manipulate perception of postural threat to increase anxiety, and to elicit the illusion of self-movement using a solely visual perturbation. VR enables placement of observers in a multitude of anxiety-inducing environments without incurring any significant physical risk, and, when compared to a 'real world' paradigm, placing someone at height in VR has comparable effects on postural control. As such, the integrity of the manipulation is largely

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preserved (Cleworth et al., 2012). Our study used a paradigm similar to that of Cleworth et al. (2016), involving the manipulation of perceived height/postural threat. To investigate the effects of incongruent sensory input on balance, a visual perturbation was used whereby the participants' viewpoint in VR environments was swayed in the pitch-up direction, and the postural reactions to this perturbation were compared between Threat levels and age groups. A physical perturbation was not included, to limit the number of trials. The current study used a paradigm that minimised the number of trials to one per condition, involving a discrete visual perturbation, in an attempt to avoid many of the aforementioned limitations related to within-trial modulation of sensory weighting (Balaban et al., 2011; Cleworth et al., 2016; Ehgoetz Martens et al., 2017; Lim et al., 2017; Staab & Ruckenstein, 2005; Staab, 2014).

Since research suggests that OAs rely more on vision than YAs to control balance (Agathos et al., 2015; Choy et al., 2003; Keshner & Slaboda, 2009; Lord & Webster, 1990; Slaboda et al., 2011), and that ageing is associated with impaired ability to maintain balance effectively during sensory disparity (Diederich, A. et al., 2008; Ramkhalawansingh et al., 2016), we predicted that OAs would show an increased postural response to a visual perturbation at both Ground and Threat compared to YAs. Given the idea that anxiety may be a significant factor contributing to these previously discussed age-related sensory processing changes, we also predicted that both young and older adults would show increased postural response in reaction to the visual perturbation (i.e., show an increased reliance on vision) at Threat compared to Ground, concurrent with an increase in self-reported state anxiety.

Materials & Methods

Participants

A cohort of 31 Young Adults (YAs) (18-30 years old, $\mu = 20.84$, s.d. = 3.26), were recruited from undergraduate and postgraduate courses at Brunel University London. A cohort of 32 Older Adults (OAs) (65-94 years old, $\mu = 77.54$, s.d. = 8.26) were recruited from community centres and local sheltered housing organisations in London. Participants in both groups had normal or corrected-to-normal vision, and no diagnosed neurological disorders. All participants were able to discuss and ask questions about the protocol and then provided written informed consent.

Equipment

Virtual environments were created as described in Chapter 2. The 'Threat' environment consisted of a platform atop a cliff overlooking a gully, with trees around the cliff top (where participants stood) and at the bottom of the gully, to provide some visual reference and enhanced distance perception. Presence of stable visual cues in close proximity to the viewer also serves to

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reduce the risk of physiological height vertigo, which has been found to destabilise postural control (Bles, Kapteyn, Brandt, & Arnold, 1980; Brandt, Arnold, Bles, & Kapteyn, 1978; Brandt, Arnold, Bles, & Kapteyn, 1980). The 'Ground' environment consisted of a large platform at ground level, again with trees placed around the participant at similar distances. Both environments contained a fixation point placed at roughly eye level – the exact position was kept consistent between the two environments (see Figure 5). The Sony HTC Vive system (1080x1200 per eye resolution, 90Hz refresh rate, 110 degrees Field of View [FoV]) was used to display the VR environments. Kinetic data were recorded at 1000Hz using a Kistler forceplate (Kistler 9287BA), with feet positioned hip-width apart in the centre of the forceplate. Data were synchronised using an analogue output from the VR software. This specified the time of perturbation onset and was recorded in parallel with forceplate data.



Figure 5. First-person views of Ground (bottom) and Threat (top) VR environments

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Procedure

Participants began each trial in a 'starting position' behind the forceplate. When given a verbal instruction, participants stepped forward onto the forceplate where the position of their feet was adjusted by an experimenter so that they were hip-width apart. The anterior edge of the forceplate corresponded with the anterior edge of the platform in the VR environment. At a randomly selected time (between 20 and 30 seconds after participants had assumed the required position on the forceplate and had received instructions to look at the fixation point, see Figure 3), participants experienced the visual perturbation described in Chapter 2: a sinusoid rotation of 5° per second, with both the pitch-up and returning pitch-down motions each lasting 1000ms. To ensure participants' safety during the experiment, they were secured in a fall-arrest harness throughout the experiment.

We included only a single perturbation (i.e., trial) within each condition to avoid potential sensory re-weighting effects that might occur once participants adapt to, or become aware of, visual-vestibulosomatosensory conflict, whereby Centre of Mass (COM) displacement and dependence on visual information reduces significantly in response to multiple perturbations following an initial perturbation (Bronstein, 1986; Bronstein, 2019; Jeka, Allison, & Kiemel, 2010; Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol et al., 2004). This limited time spent in VR to under 2 minutes per condition, which also minimised the degree to which participants became familiar with the Threat environment, in an attempt to minimise any habituation to the threat that may incur downweighting of vision (Nishiike et al., 2013; Wuehr et al., 2019). The order of conditions was counterbalanced to account for the possibility that participants would start to predict the occurrence and/or timing of perturbation in the second trial. After each perturbation, while still viewing the VR environment, participants completed a verbal state anxiety self-report; the Mental Readiness Form (MRF) (Krane, 1994). The MRF uses three questions regarding feelings of worry (cognitive anxiety), body tension (somatic anxiety), and confidence, scored on a scale of 1 to 11³.

*Analysis***Anxiety**

In this study, the three MRF scores were summed to give a maximum possible score of 33, with higher scores reflecting greater state anxiety.

³ Note, since a higher score in response to the confidence question denotes less state anxiety, the confidence subscale was reverse coded so that summing the scores gives a score where high scores represent increased anxiety.

COP Data

Data were filtered (second order low-pass Butterworth filter with a cut-off frequency of 5Hz) in MATLAB (The Mathworks Inc., 2017), and characteristics of participants' COP displacement following the visual perturbation was evaluated by selecting filtered data from a six-second time window starting at three seconds prior to perturbation onset. The value of each participant's mean position during the three seconds prior to perturbation onset was subtracted from the position of their anterior peak occurring within the first 1000ms following perturbation onset, giving the primary outcome measure of Relative Anterior Peak (RelAP). This variable expresses the amplitude of initial anterior sway response as participants attempt to correct for their perceived posterior motion. Given that foot position is difficult to control when using VR, we avoid direct comparison of absolute values. Following work by Keshner and Slaboda (2009), we expect that RelAP will increase during Threat due to the hypothesised increased reliance on visual information with anxiety. We also expect that those in the OA group will show an increased overall response compared to YAs.

To gain additional insight into the spatiotemporal nature of COP responses that contribute to the postural response, we isolated other specific components of the COP response. The time taken to reach their anterior peak (AP Latency) was analysed between conditions and groups. Previous research has found Threat-related decreases in the time taken to reach peak position in response to a perturbation (Cleworth et al., 2016; Sibley, Mochizuki, Frank, & McIlroy, 2010), and that age tends to increase this latency of response (Lin, S. & Woollacott, 2002). Therefore, in young adults, we expect that AP Latency will be reduced in Threat compared to Ground; this may also occur in OAs, but we do expect a longer latency overall in this group given previously demonstrated age-related latency increases (Lin, S. & Woollacott, 2002). See Table 3 for means and standard deviations of each measure, and Figure 6 for a graphical representation of these measures.

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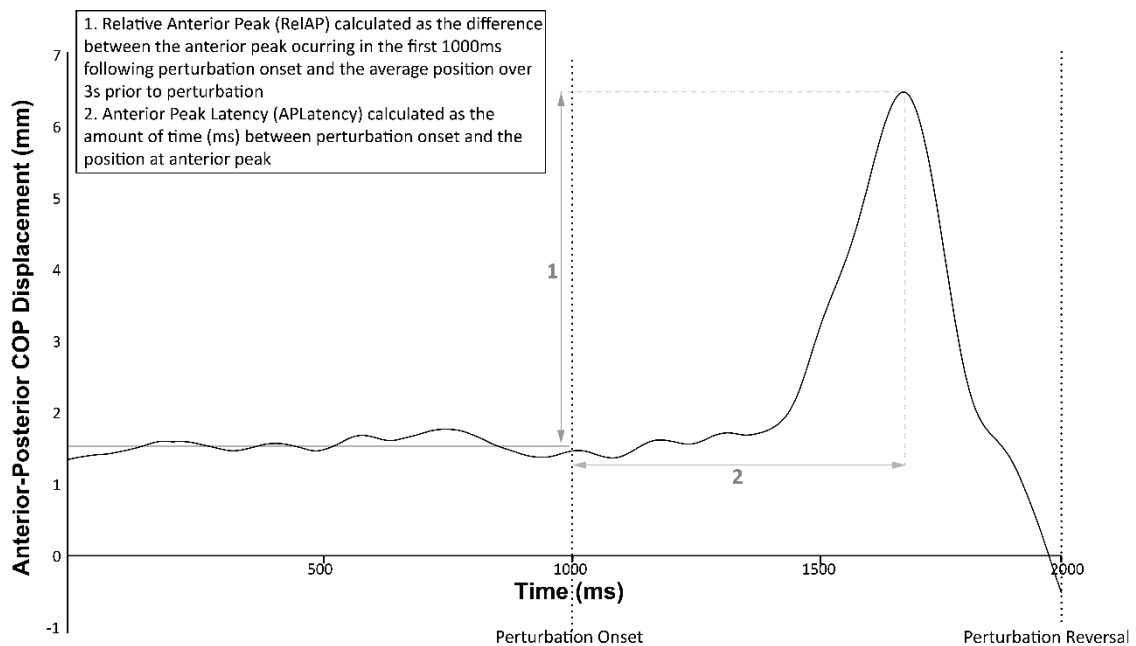


Figure 6. A graphical representation of the outcome measures and the angular displacement of the visual perturbation used in this study.

Statistics

For each case where data were non-normally distributed, we performed a log transformation. Where data became normal, the log transformed data were entered into an appropriate ANOVA with Bonferroni correction. Where data remained non-normal after log transformation, we used non-parametric tests on the original data, which tested for differences between conditions within each age group, and between age groups, for each condition. Any outliers/participants with z-scores over 3 (or less than -3) for any measure were removed from analysis of that measure.

MRF data were not normally-distributed and were not made normal following log-transformation. Therefore, non-parametric tests were used to compare results between groups and conditions. RelAP data were not normally-distributed but became so following log transformation and adding a constant to each value to allow for log-transformation of negative values, therefore were analysed using a mixed ANOVA. AP Latency data were not normally-distributed for either group; log transforming was unsuccessful, therefore appropriate non-parametric tests were used to analyse differences between conditions and groups.

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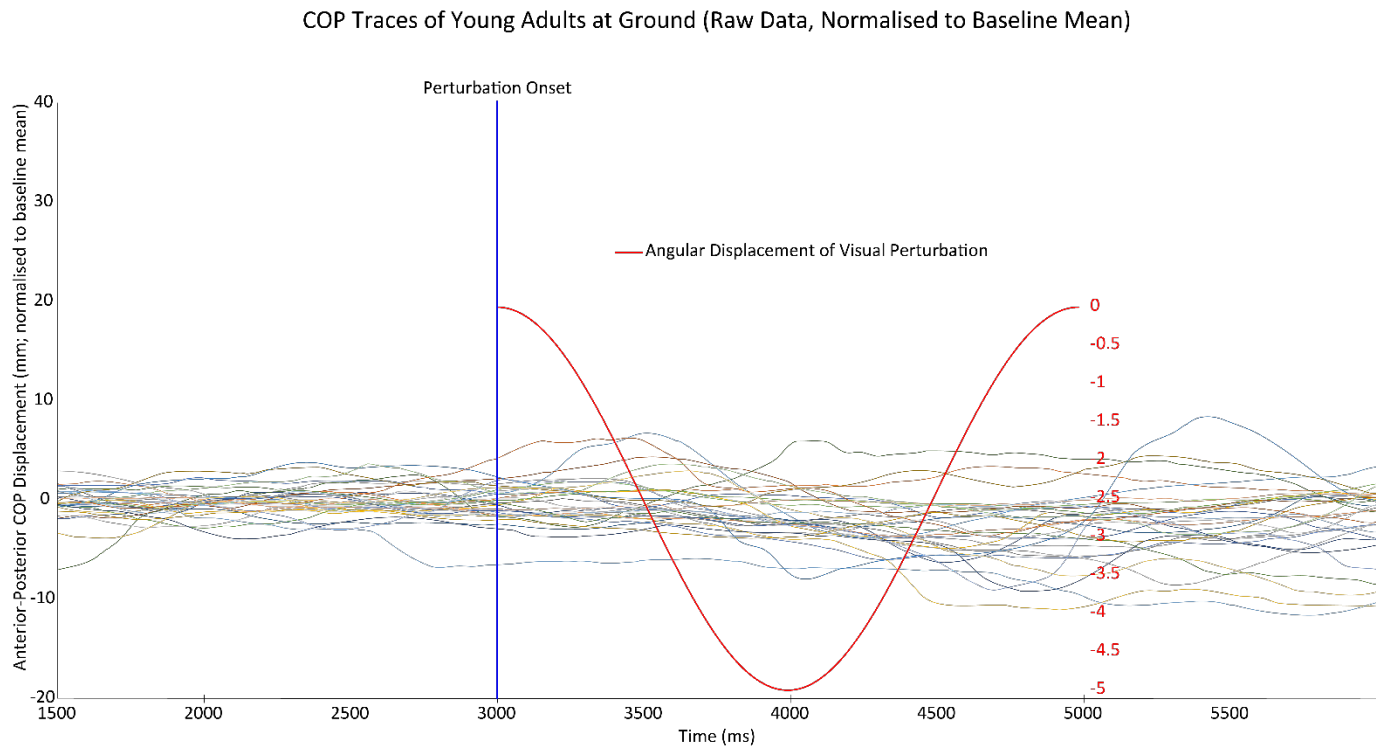


Figure 7. Raw traces of young adults' anterior-posterior COP displacement during quiet standing and during the perturbation at Ground, normalised to the 3s baseline mean with overlaid perturbation waveform. Values in red indicate Euler angles.

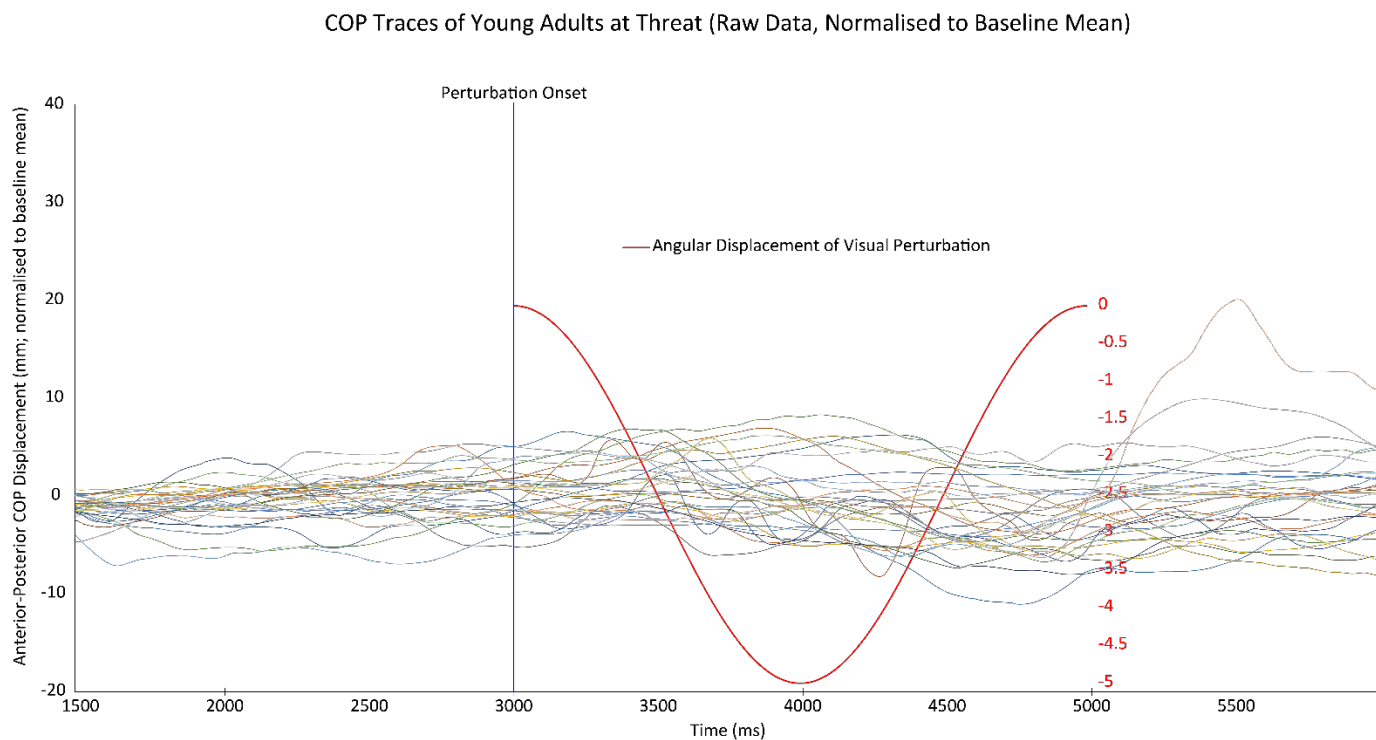


Figure 8. Raw traces of young adults' anterior-posterior COP displacement during quiet standing and during the perturbation at Threat, normalised to the 3s baseline mean with overlaid perturbation waveform. Values in red indicate Euler angles.

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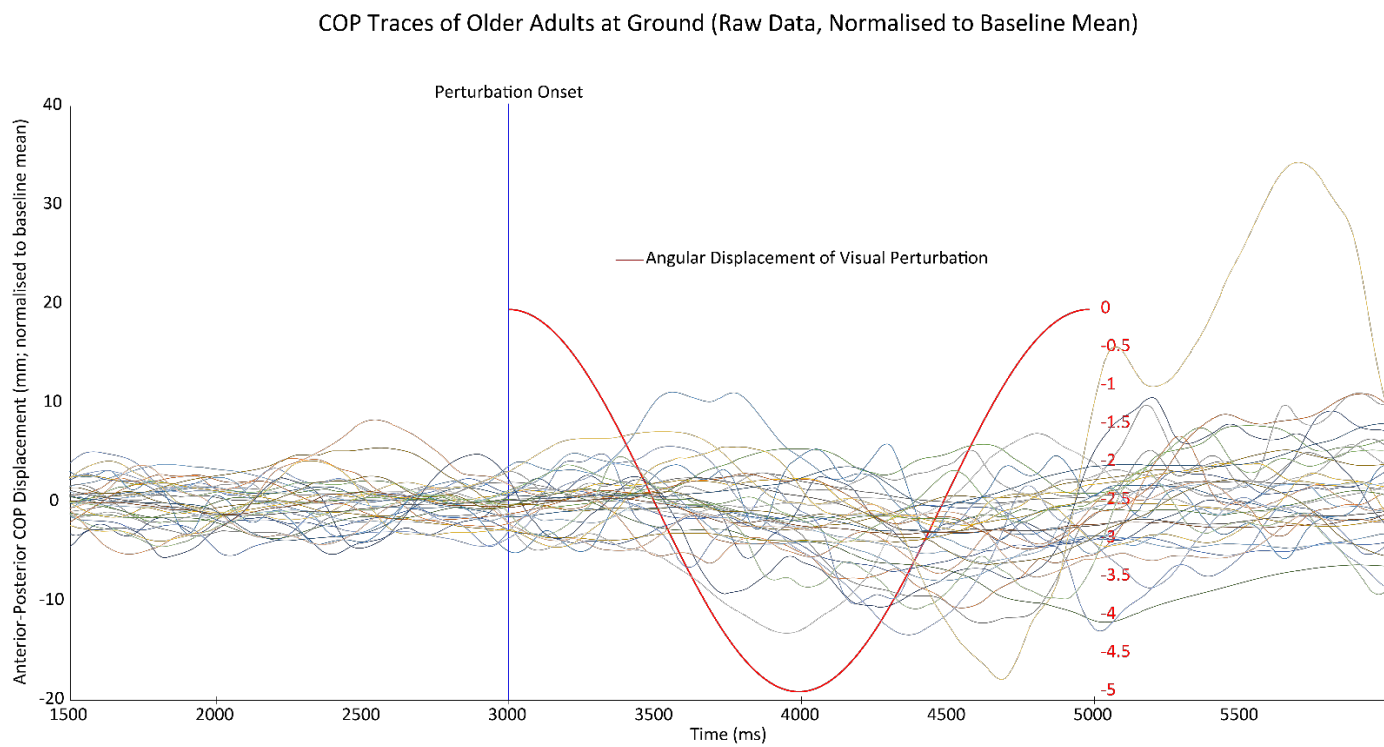


Figure 9. Raw traces of older adults' anterior-posterior COP displacement during quiet standing and during the perturbation at Ground, normalised to the 3s baseline mean with overlaid perturbation waveform. Values in red indicate Euler angles.

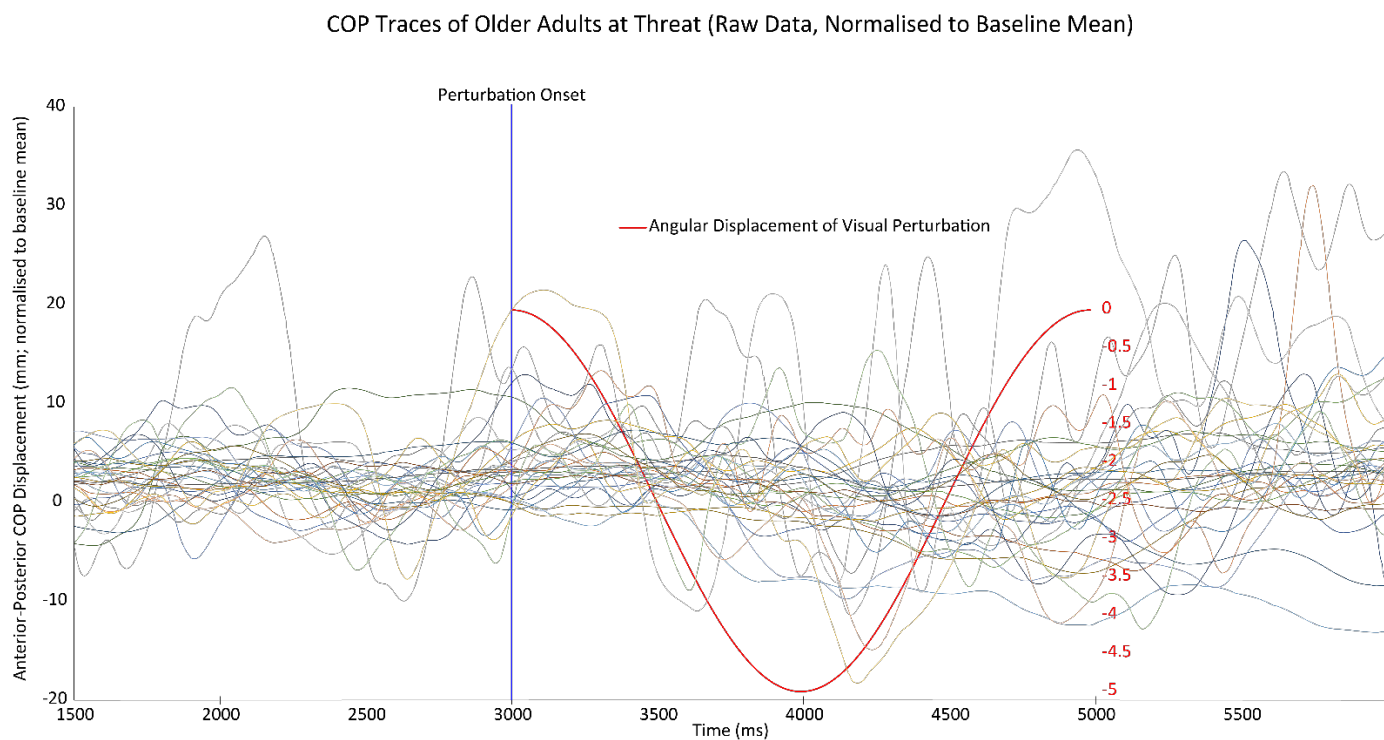


Figure 10. Raw traces of older adults' anterior-posterior COP displacement during quiet standing and during the perturbation at Threat, normalised to the 3s baseline mean with overlaid perturbation waveform. Values in red indicate Euler angles.

Results

Anxiety

Results showed a significant effect of Threat condition, with both age groups reporting significantly strongly increased state anxiety during Threat compared to Ground ($p < 0.001$, $Z = 3.916$, $r = 0.715$ for YAs; $p < 0.001$, $Z = 4.543$, $r = 0.844$ for OAs; Wilcoxon Signed Rank Tests, alpha = 0.025). No effect of Group was found at either Ground ($p = 0.607$, $Z = 0.515$, $r = 0.07$) or Threat ($p = 0.519$, $Z = 0.645$, $r = 0.08$; Mann-Whitney U Tests, alpha = 0.025).

RelAP (Relative Anterior Peak)

A mixed ANOVA revealed a main effect of Threat ($F(1, 57) = 12.55$, $p = 0.001$, $\eta_p^2 = 0.18$), i.e., both groups showed significantly increased anterior peak relative to mean baseline position at Threat compared to Ground. There was also a main effect of Group, where OAs showed significantly increased RelAP across conditions compared to YAs ($F(1, 57) = 5.88$, $p = 0.019$, $\eta_p^2 = 0.093$). There was no interaction between Group and Threat conditions ($F(1, 57) = 0.348$, $p = 0.558$, $\eta_p^2 = 0.006$). See Figure 5.

AP Latency

In YAs, the AP response latencies were significantly moderately increased at Threat compared to Ground ($p = 0.023$, $Z = 2.277$, $r = 0.409$). This effect was not observed in OAs ($p = 0.813$, $Z = 0.237$, $r = 0.043$; Wilcoxon Signed Rank Tests, alpha = 0.025). However, there were no observed group differences at either Ground ($p = 0.293$, $Z = 1.051$, $r = 0.134$) or Threat ($p = 0.176$, $Z = 1.353$, $r = 0.172$; Mann-Whitney U Tests, alpha = 0.025).

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Table 3. Means and standard deviations for each measure of COP response and state anxiety

Group	Condition	RelAP (mm)	AP Latency (ms)	State Anxiety (max. score = 33)
YAs	Ground	1.10 (2.47)	358.81 (329.35)	5.10 (3.13)
	Threat	3.14 (3.14)	559.81 (385.71)	13.27 (8.46)
OAs	Ground	2.59 (2.66)	447.97 (348.00)	5.90 (4.17)
	Threat	4.63 (4.57)	427.29 (316.06)	14.93 (9.06)

Values are in the form of μ (s.d.). * indicates significance at alpha level 0.017; ** indicates significance at alpha level 0.01; *** indicates significance at alpha level 0.001.

Correlational Analyses

Given the non-normally distributed nature of the Anxiety data, Spearman's rho correlations were performed to check for correlations between state anxiety levels and postural behaviour. In YAs, there were no significant correlations between RelAP and Anxiety at either Ground or Threat. In OAs, these variables were significantly moderately correlated at Threat ($p = 0.013$, $r = 0.413$), but not at Ground (see Table 4). There were no correlations in either group between Anxiety and AP Latency.

Table 4. Results of the correlational analysis between several outcome measures in both groups in both conditions.

Group	Condition	Anxiety/RelAP	Anxiety/AP Latency
YAs	Ground	0.261; 0.086	0.028; 0.443
	Threat	-0.006; 0.487	-0.151; 0.213
OAs	Ground	-0.065; 0.369	-0.302; 0.056
	Threat	0.413; 0.013*	-0.102; 0.299

Values are one-tailed Spearman r followed by the p -value. * indicates significance at alpha level 0.017.

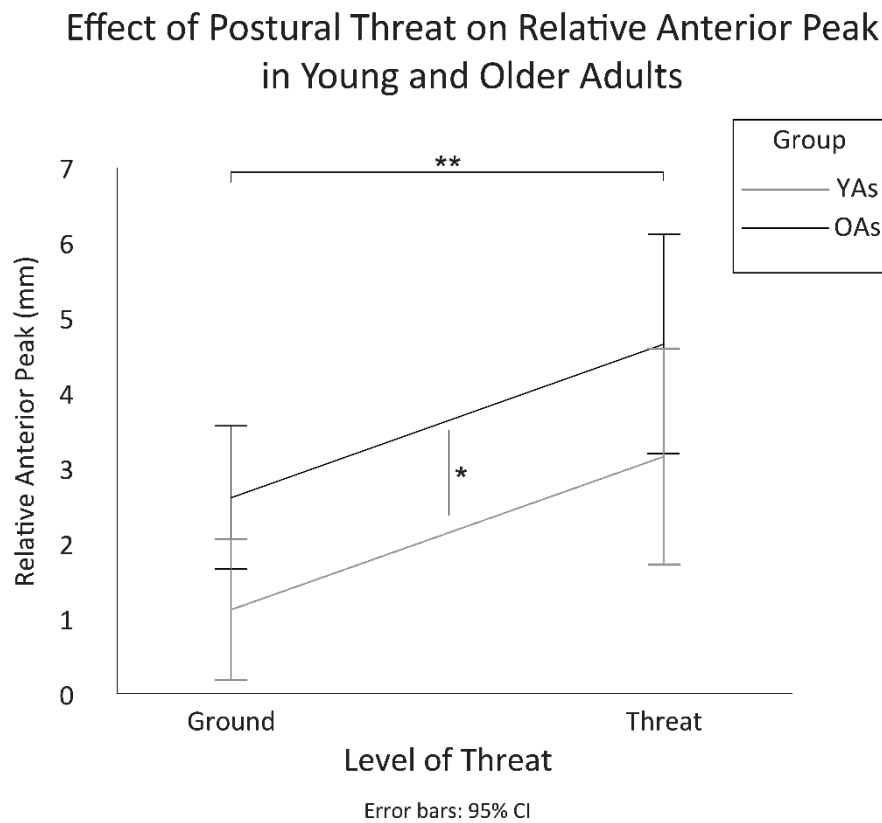


Figure 11. Line graph of mean RelAP (pre-log transformation) for YAs and OAs at both Ground and Threat, showing a significant increase in RelAP with both Threat and Age. * indicates significance at alpha level 0.05; ** indicates significance at alpha level 0.01.

Discussion

The primary aim of the current study was to investigate whether anxiety is a significant factor contributing to changes in sensory reweighting. To this end, this study examined whether a heightened perception of postural threat serves to increase reliance on vision to maintain balance, as measured through the behavioural sway response to a visual perturbation. By utilising a discrete visual perturbation paradigm to separate visual and non-visual sensory inputs, this study is the first to show direct evidence for increased state anxiety eliciting greater reliance on vision, resulting in a destabilising effect on orthostatic balance control. This discussion will first review the overall effects of postural threat on visual reliance, followed by a discussion of the observed age effects.

Increased Reliance on Vision with Postural Threat

Our primary outcome measure of Relative Anterior Peak (RelAP) indicates a significantly increased response to the visual perturbation at Threat compared to Ground, suggesting a significant effect of increased state anxiety on visual reliance. These observations are in line with previous findings that indicated an increase in visual reliance with anxiety (Jacob et al., 1995; Jacob et al., 2008), but provide direct evidence in a manner that is less susceptible to reweighting. Concurrent

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with this measure, the latency of response was increased at Threat compared to Ground in YAs. Previous studies have observed *reduced* latencies with postural threat (Cleworth et al., 2016; Sibley et al., 2010). Presumably, in the current study, the effect of postural threat on the magnitude of the anterior peak response on YAs was great enough that these participants took longer to reach their anterior peak compared to ground.

The protocol of relying on only a single trial (i.e., perturbation) per condition is potentially volatile, and interferes with the ability to make more definitive conclusions about individual responses. Previous studies in this field use continuous oscillating visual perturbations paired with longer trials (Slaboda et al., 2011) that allow for more reliable interpretation of individual mean responses. However, Jeka, Allison, and Kiemel (2010) demonstrated down-weighting of visual input during repeated visual perturbations in trials of shorter duration than those used by the aforementioned studies. While we acknowledge that discrete perturbations and limited trial protocols (as employed here) present their own challenges and confounds, we also argue that this approach largely bypasses the issue of progressive down-weighting of visual input that presumably occurs when this information is deemed unreliable following prolonged trials with repeated perceptible perturbations (Bronstein, 2019; Shumway-Cook & Horak, 1990). As such, we argue that increased perceived postural threat does indeed increase visual reliance, and that the outstanding questions now relate to factors that influence the rate of down-weighting.

Effects of Ageing

Our second main conclusion is that Older Adults (OAs) appear to rely more on vision for balance control than YAs, even in the absence of postural threat. This conclusion is driven by group differences observed across outcome measures. First, we observed significantly greater RelAP in OAs compared to YAs across both conditions, indicating a greater reliance on visual input for self-motion information. While there was no significant group effect in AP Latency, this measure was significantly increased by Threat in YAs, but not OAs. This could indicate age-related differences in how the processing of incongruent sensory inputs is affected by increased anxiety. Others have demonstrated that OAs are less tolerant of incongruent sensory cues (Berard, Fung, & Lamontagne, 2011; Deshpande & Patla, 2007) whereby they are less able to integrate multiple inputs as effectively as YAs to maintain balance. Basharat, Mahoney, and Barnett-Cowan (2019) suggest decline in GABA concentration as a potential culprit in age-related multisensory processing deficits, particularly when attempting to judge the temporal order of different senses (Lupo & Barnett-Cowan, 2018). In the current study, these differences could be influencing postural performance at Ground, resulting in less capacity for change in OAs' postural behaviour between Ground and Threat

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i.e., a ceiling effect. We speculate that, since OAs are potentially less able to distinguish relevant sensory signals from noise (Mozolic et al., 2012), OAs may have taken longer to process the incoming discrepant sensory information (Diederich, A. et al., 2008), leading to a delay in response, even at Ground. However, increased response amplitudes observed in OAs' RelAP suggest that, once the sensory discrepancy has been 'detected', OAs rely more on visual than non-visual input. These results could be indicative of a 'ceiling effect', whereby RelAP was already at a sufficiently large amplitude at Ground that the increase in state anxiety at Threat had relatively little effect. This suggests that the observed Threat-related changes in YAs could be predominantly responsible for driving the main effect of Threat on RelAP magnitude (see Figure 11).

A relationship was observed between sway response and anxiety, as demonstrated by the significant correlations between RelAP and state anxiety whereby these postural responses were higher when participants reported greater anxiety. However, this correlation was only significant in OAs. While this may be due to a lesser range of values in YAs, we suggest that, for OAs, anxiety about falling may represent an emotion that is more meaningful and representative of that encountered in daily life (Legters, 2002; Scheffer et al., 2008). As such, during Threat trials where participants self-report greater anxiety (see Table 1), OAs may have employed mechanisms (e.g., for consciously controlling movement) that represent familiar changes in attention and balance control (Ellmers et al., 2019b). As suggested by previous work (Eikema et al., 2013; Hawkes et al., 2012), this may have contributed to an increased reliance on vision and therefore increased RelAP in response to the visual perturbation.

With no discernible differences between groups in anxiety levels in the present study, group differences in postural response measures indicate that age-related factors (other than anxiety) are primarily responsible for driving increased reliance on vision (Choy et al., 2003; Diederich, A. et al., 2008; Hausdorff et al., 2001; Horak et al., 1989; Tinetti et al., 1988), even in our relatively healthy, low-risk older group. Recent research has attempted to further elucidate how sensory reweighting during balance maintenance is affected by ageing. Ramkhalawansingh et al. (2018) found age-related decline in visual-vestibular integration during self-motion perception, albeit not in the context of heightened anxiety. Jeka et al. (2010) demonstrated increased reliance on visual information in older adults compared to younger adults, and showed that older participants are slower at reweighting visual information when exposed to high amplitude visual stimuli. This difference was also apparent between healthy older adults and their age-matched fall-prone cohorts, where fall-prone OAs were even more reliant on vision than OAs at a low risk of falling. Alberts, Selen, and Medendorp (2019) suggest that this age-related increase in visual reliance may be due to increased noise in the vestibular system. These age-related changes in sensory processing

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could explain the group differences observed in the current study, whereby factors such as increased vestibular noise in the OA group could have resulted in their increased reliance on vision, thus their increased response to the visual perturbation even in the absence of anxiety at Ground.

An additional explanation for age-related differences in observed postural responses between conditions relates to where participants allocated attention. Some argue that attention may be a key factor in mediating the effects of anxiety/postural threat on balance control (Adkin & Carpenter, 2018; Zaback, M., Carpenter, & Adkin, 2016). Increasing postural threat by raising participants 3.2m above ground level produces an increase in self-reported conscious control of, and concern about, posture, compared to when standing at ground level (Adkin & Carpenter, 2018).

Following this work, Zaback, Carpenter, and Adkin (2016) found increased allocation of attention to self-monitoring of movement and self-regulatory strategies at height (compared to ground). The authors suggested that allocating attention towards self-body movement may represent a priming of 'bottom-up' processes, since other research indicates gain increases in proprioceptive (Davis et al., 2011) and vestibular (Naranjo et al., 2015) inputs with postural anxiety (not specific to increased conscious control). Furthermore, Reynolds (2010) demonstrated that conscious control of movement can attenuate long-latency vestibular-evoked postural responses, i.e., voluntary conscious regulation of postural control can directly influence output from the vestibular system. Since OAs are more likely to consciously monitor and control movement (Boisgontier et al., 2013; Chow et al., 2018) it is possible that the OAs in the current study increased the conscious monitoring/control of their movement during both conditions, eliciting changes in the gain of different sensory inputs, thus resulting in increased visual reliance/postural response compared to YAs.

Limitations

The mean response latencies observed in this study are greater than those typically discussed in previous literature (Cleworth et al., 2016; Keshner & Slaboda, 2009; Lin, S. & Woollacott, 2002). However, the visual perturbation used in the current study was much slower than those in previous studies (Keshner and Slaboda (2009), for example, used perturbations occurring at a speed of 30°/s – six times faster than the perturbation in the current study). Combined with the sinusoidal nature of this perturbation, this suggests that the responses seen at these latencies were visually driven. Furthermore, given that this particular perturbation type has not been used in previous studies, there was no specific precedent for removing responses occurring at any given time from analysis. It is important to note that perceptual integration of multimodal stimuli is not a linear process; studies have shown that even young, healthy individuals reweight these inputs

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differentially (Streepey, Kenyon, & Keshner, 2007). Again, given the relatively novel nature of the perturbation characteristics utilised here, it is difficult to characterise/classify between-subject differences in response to the perturbation (such as early vs. late responses that may indicate more vs. less visual dependence), since there is little precedence in the current paradigm to classify these potential groups. While conducting a rod-and-frame test prior to the VR session may have given some insight into individual levels of visual dependence, these scores are not typically correlated with subsequent postural reactions to perturbations/visual flow stimulations (Slaboda et al., 2011), and therefore would not be useful for categorising participants' postural responses in this context. Another limitation is the use of a perturbation that contains a reversal in direction after the first 1000ms of posterior motion. While this was designed to be representative of a real-life momentary loss of balance, this prevents analysis of postural behaviour in the latter half of the perturbation period, since we cannot determine whether the subsequent post-reversal postural behaviour is influenced by attempts to return to upright standing or continued visual influence of the perturbation. Future studies may endeavour to optimise the use of visual stimuli in VR to accurately measure postural responses without such confounding factors while still avoiding potential effects of habituation or loss of realism.

All participants using vision-correcting equipment (e.g. glasses, contact lenses) wore them in the VR environment. Since the main comparison in this study related to a within-subjects design, the nature of corrected vision remains consistent across comparisons. One potential issue is that more OAs wore glasses than YAs, and it is possible that the frames of the glasses may have caused some occlusion of the peripheral visual field. However, by partially obscuring peripheral vision, one would expect participants to show attenuated postural responses to the visual perturbation by virtue of the reduced saliency of the perturbation, relative to other available sensory information. On the contrary, since OAs showed an *increased* sway response, we do not consider the fact that more participants wore glasses in this group to be a major confound. Avoiding the use of corrective lenses in older cohorts represents a logistical challenge and could introduce issues relating to recruitment bias; it is hoped that future work may endeavour to account for this issue through use of in-built corrective lenses within the VR headset.

As a study on the effects of postural threat during orthostatic balance, the extent to which these findings can be extrapolated to interpret behaviours observed during gait are limited, but future research combining a dynamic task such as treadmill walking with postural threat in VR could elucidate this issue of how sensory reweighting during locomotion might be affected by increased state anxiety. Similarly, in the absence of any direct measure indicating how other senses were utilised, we are limited to drawing conclusions related to increased visual reliance, and not reliance

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on specific proprioceptive or vestibular input. Previous research has demonstrated that increased postural threat results in upregulation of proprioceptive signals (e.g. muscle spindle sensitivity (Horslen et al., 2013) and increased perception of sway (Cleworth & Carpenter, 2016)). We speculate that, while these incoming non-visual signals are subject to anxiety-related gain increases (Cleworth & Carpenter, 2016; Davis et al., 2011; Horslen et al., 2013; Horslen et al., 2014; Lim et al., 2017), the CNS still down-regulates their relative contribution during the integration process in favour of prioritising visual input. Since voluntary control of movement can modulate balance-related vestibular responses, it would be informative to focus future efforts on evaluating whether explicit manipulation of attention (either inward i.e., movement processes/proprioception, or outward i.e., visual cues) might change sensory re-weighting during periods of anxiety and discrepant sensory input.

Conclusions

Our findings indicate that perception of increased postural threat leads to increased reliance on vision to control balance. Our results strengthen the foundation for concluding that a causal link exists between increased anxiety and visual reliance, and support the use of a limited-trial paradigm for investigating the effects of postural threat on visually-evoked postural responses. This study also demonstrates an age-related increase in postural sway in response to sensory incongruence, with an age-related increase in visual reliance that is not fully explained by increased anxiety, thereby prompting further suggestions for alternative factors that may be responsible for intolerance of sensory disparity and (ultimately) impaired balance control. While previous studies have drawn similar conclusions, we argue that they have only ever been founded on indirect evidence and/or using longer trial durations with continual perturbations, where participants could potentially reweight their reliance between senses during the trial, or excluded the use of postural threat. The current study represents the first instance where a single trial per condition protocol containing a discrete perturbation has been used, thus providing direct evidence for increased visual reliance while largely avoiding the main confounds present in previous work. Future research in this field would benefit from investigating the temporal nature of reweighting visual input in favour of other senses during sensory discrepancy.

Chapter 4.

Study 2: The Effect of Postural Threat on Visual Reliance for Balance Control in a Clinical Setting: Parkinson's Disease

In Chapter 3, we observed that older adults (OAs) display postural behaviour consistent with more reliance on vision than younger adults (YAs) despite comparable levels of self-reported anxiety, and even in the absence of postural threat. Therefore, it appears that other age-related changes in sensory integration may be influencing the upweighting of vision.

As previously described in Chapters 1 and 3, sensory integration literature suggests impairments in some senses may lead to upweighting of others. This is particularly relevant in neurodegenerative diseases such as Parkinson's, characterised by deficits in the motor system and sensory inputs relevant to self-motion. In this neurodegenerative disease, a reduction in dopamine production from the basal ganglia produces debilitating paucity of movement, which may be manifested through tremors, bradykinesia (slowness of movement), and akinesia (lack of normal movement) (Nieuwboer, Weerdt, Dom, & Lesaffre, 1998).

Proprioceptive Deficits in Parkinson's Disease

A decline in proprioceptive function is typical in PD (Konczak et al., 2009), both as a result of the basal ganglia damage from the disease itself (Maschke, Gomez, Tuite, & Konczak, 2003; Maschke, Tuite, Krawczewski, Pickett, & Konczak, 2006) and possibly because of the dopaminergic medication taken to reduce parkinsonian symptoms (O'Suilleabhain, Bullard, & Dewey, 2001). A review by Konczak and colleagues (2009) discusses the impairments in the basal ganglia resulting in noisy and abnormally-timed signals propagating to the motor system, leading to a downweighting of proprioceptive input. This impairment in proprioceptive function is likely to elicit a larger reliance on non-proprioceptive input such as vision (Bronstein, 2019; Butler et al., 2010; Knill & Pouget, 2004).

These deficits (and subsequent effects) are apparent in studies on sensory reweighting and postural behaviour. Bronstein, Hood, Gresty, and Panagi (1990) compared the postural response to a visual perturbation between PD patients and healthy controls. Participants stood on an earth-fixed platform, which measured centre of force displacement in a room with movable walls. In controls, sway was attenuated during the second perturbation compared to the first perturbation. PD patients, in contrast, were not able to attenuate their body sway despite repeated exposure to the perturbation. This, argue Bronstein and colleagues, illustrates how, in order for a response to an erroneous sensory signal to be suppressed, information from a different reliable source must be able to be processed. In this case, healthy adults can suppress the response to visual stimulus because

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their proprioceptive system is able to correctly process incoming proprioceptive signals, thus restoring balance control appropriate for the situation. However, for those with PD, the proprioceptive system is impaired, thus proprioceptive information is not available for use of stabilising the body once visual input is deemed unreliable. Therefore, the reliance remains largely on the visual system, resulting in VEPRs that are no smaller than in response to the first presentation. This suggests that PD patients are less able to recruit proprioceptive input for balance control when other senses (such as vision) are erroneously incongruent with inertial cues. It is also worthwhile to note that while deficits in low-level vision have also been well-documented in Parkinson's Disease (Bodis-Wollner et al., 1987; Bulens, Meerwaldt, Van der Wildt, & Van Deursen, 1987; Diederich, N. J., Raman, Leurgans, & Goetz, 2002; Weil et al., 2016) these are unlikely to affect self-motion perception (Halperin et al., 2020). Thus, it is unlikely that these visual deficits would dissuade the sensory integration system from relying on vision as opposed to impaired proprioception.

Freezing of Gait

This is particularly problematic for a subset of PD patients who also suffer from a specific symptom called "Freezing of Gait" (FOG), characterised by a compromised ability to initiate or continue self-generated movement, particularly walking (Hausdorff et al., 2003; Vandenbossche et al., 2013). While Bronstein and colleagues' study (1990) shows the impact of PD in a basic environment, it did not include a manipulation of anxiety, which seems to be particularly problematic for PDs with FOG (PD+FOG; (Witt, Ganjavi, & MacDonald, 2019). Many studies have found a positive association between anxiety levels and FOG severity (Lieberman, 2006; Pimenta et al., 2019; Walton et al., 2015). Furthermore, manipulating anxiety in PD patients with FOG exacerbates motor symptoms; Ehgoetz Martens, Ellard, and Almeida (2013) exposed PD patients (with and without FOG) to both a non-threatening and a threatening (being placed at height) VR environment. Participants were instructed to walk while their gait was recorded. Those with FOG experienced significantly increased motor symptoms during the threatening environment than the non-threatening, while those without FOG had comparable gait characteristics across both environments. In subsequent research, rather than examining motor symptoms associated with PD+FOG, it remains to be seen if these manipulations of anxiety will influence visual reliance. If so, any observed changes in reweighting might be implicated in contributing to motor symptoms in PD+FOG.

While several recent studies suggest persistent upweighting of vision in PDs compared to healthy OAs and YAs, these studies use multiple and/or repeated trials (e.g. (Yakubovich et al.,

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2020). Therefore, it is unclear what happens during an unexpected perturbation without the possible confounds of repeated exposure to the sensory incongruence – especially in with those with FOG. The current study is novel in that it uses a single perturbation (i.e., experience of vection) per condition. The novelty of using a single perturbation avoids the potential confounding factors of using repeated trials – namely habituation to the stimulation. As trials are repeated, the observed behaviour may mask any initial reweighting effects that could be present during the first/early unexpected (part of the) stimulation.

Aims & Hypotheses

Since postural anxiety has been demonstrated to elicit altered sensory reweighting ((Cleworth et al., 2012; Cleworth & Carpenter, 2016; Cleworth et al., 2016); Chapter 3), and to be particularly problematic for PD patients with FOG (see Chapter 1; (Ehgoetz Martens et al., 2017)), it would be beneficial to discover a) whether increased reliance on vision in PD patients with patients with FOG compared to healthy controls will still be observed in a VR environment using a limited-perturbation paradigm (where the visual perturbation is sudden/unexpected, therefore mitigating habituation effects), and b) how this effect might be exacerbated by increased anxiety; we might expect a particularly strong VEPR in PD patients with FOG during postural threat compared to their healthy cohorts. With the pathogenesis of FOG not being well-understood, and the relative ineffectiveness of treatments (Nutt et al., 2011), there is clearly a need for more in-depth understanding of the underlying mechanisms of sensory reweighting in PD+FOG. This, ideally, will lead to more effective interventions and therapeutic techniques to improve quality of life from people with PD and FOG.

Therefore, the aim of the current experiment is two-fold. First, we aim to examine the effect of sensory disparity on VEPRs in a population affected by proprioceptive and motor impairments compared to healthy controls, who have arguably less propensity to rely on vision compared to PDs with FOG. Second, to look at relevant effects of postural threat in this patient population, which will also be compared to their healthy cohorts. The current experiment uses the original paradigm as described in the previous chapters. We first hypothesise that PDs with FOG will rely more heavily on vision than their healthy equivalents, and that this will be manifested through increased COP displacement (primarily an initial anterior COP response to the pitch-up perturbation) in participants with PD+FOG compared to healthy controls in a ground-level environment. Second, we predict that this effect will be exacerbated by changes in balance-related sensory reweighting precipitated by postural threat, with the PD+FOG group showing a larger increase in COP measures and self-reported state anxiety than healthy controls.

Materials & Methods

Participants

23 people with Parkinson's Disease, who all reported some degree of Freezing of Gait (PD+FOG), were recruited via various Parkinson's Disease support and research groups throughout the UK. The age group ranged from 48 to 83 (μ : 70.98, s.d.: 8.56). All participants in the PD+FOG group completed the experiment between one and two hours after medication dosage (i.e., during the ON state). Twenty-three healthy age-matched older adults (OAs) were primarily recruited through Brunel Older people's Reference Group (BORG), with a few participants recruited via their accompaniment of PD+FOG participants. All PDs completed the FOG questionnaire (Giladi et al., 2000), and the Montreal Cognitive Assessment (MoCA; (Nasreddine et al., 2005)). All PD patients scored at least 22 on the MoCA, above the threshold for cognitive impairment (Trzepacz et al., 2015). While we were unable to recruit a non-FOG PD group for comparison, the FOG questionnaire allows for correlation analysis to assess any within-group effects of FOG severity on postural behaviour. Since the study paradigm required participants to be able to step safely on and off a forceplate and stand unaided (other than the safety harness), all PD participants participated in the study during the "on" state of their PD medication. While an "on" state may mask some between-subject differences that we may see in "off" state PD participants, the stress that may have been experienced by PD participants caused by movement difficulties usually ameliorated by medication would arguably have confounded our results. Approval to conduct the study was obtained from the Brunel University Ethics Committee, and all participants gave written informed consent.

Equipment

Equipment remained the same as the previous study; see Chapter 3.

Procedure

The procedure followed that of the previous experiment/chapter – two trials, one at Ground and one at Threat, each consisting of a short period of quiet standing in the VR environment followed by a 2-second visual perturbation (1 second sinusoid movement of 5 degrees in the pitch-up direction followed by a second sinusoid movement of 5 degrees in the pitch-down direction back to upright). As previously mentioned, prior research has used paradigms involving repeated and/or prolonged presentations of perturbations and/or sensory incongruence. While multiple/prolonged trials obviously increase the power of the observed results, this method risks confounding the findings with reweighting that may occur over multiple or long trials (Bronstein, 1986; Bronstein, 2019; Jeka et al., 2010; Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol et al., 2004). Thus, the

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perturbations (i.e., trials) were limited to one per condition. Each trial was followed by verbal completion of the Mental Readiness Form (MRF) questionnaire (Krane, 1994).

Analysis

Measured variables remained the same as the previous experiment/chapter. Self-reported anxiety levels during each condition were measured through scores given on MRF following each trial. Relative Anterior Peak (RelAP) was the measurement of initial compensatory movement (in the anterior-posterior plane) in reaction to the initial pitch-up motion of the visual perturbation. This served as a measure of reliance on visual information. Anterior Peak Latency (AP Latency) was the measurement of time taken to reach the anterior peak following the perturbation onset, and served as a measure of response time to the stimulation.

Statistics

Where data were non-normally distributed, they were log transformed. If successful, the transformed data were entered into appropriate parametric analyses. If not, appropriate non-parametric analyses were applied. Any multiple comparisons received appropriate corrections, and any outliers were removed from the relevant analysis.

Results

Anxiety

Non-parametric analyses revealed a significant effect of Threat on MRF scores for both groups (PDs: $p = 0.001$, $Z = 3.405$, $r = 0.743$; OAs: $p < 0.001$, $Z = 3.728$, $r = 0.814$; Wilcoxon Signed-Rank tests). There were trends towards PDs reporting higher levels of state anxiety than OAs at both Ground ($p = 0.042$, $Z = 2.033$, $r = 0.314$) and Threat ($p = 0.04$, $Z = 2.055$, $r = 0.317$), but these were not significant after adjustment for multiple comparisons.

RelAP (Relative Anterior Peak)

A Mann-Whitney U test revealed no effect of Group at Ground ($p = 0.318$, $Z = -1$, $r = 0.209$). This result was also true for Threat ($t(44) = 0.187$, $p = 0.853$). No effect of Threat was found for either PDs ($p = 0.503$, $Z = 0.669$, $r = 0.140$; Wilcoxon Signed-Rank test) or OAs ($t(22) = 2.082$, $p = 0.049$; not significant following adjustment for multiple comparisons). A Levene's test of equality of variances showed a violation at Ground, with variability being greater in the PD group than in the OAs.

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AP Latency

A mixed ANOVA showed no effect of Threat ($F(1, 44) = 1.941, p = 0.171, \eta_p^2 = 0.042$), but a main effect of Group was significant ($F(1, 44) = 5.857, p = 0.020, \eta_p^2 = 0.117$), with PD patients showing a larger delay between perturbation onset and subsequent postural reaction compared to OAs. There was no significant interaction between Threat and Group ($F(1, 44) = 0.891, p = 0.350, \eta_p^2 = 0.020$).

Table 5. Means and standard deviations (of original non-log-transformed data) of state anxiety at both levels of threat, for both PDs and OAs.

		RelAP (μ (sd); mm)	AP Latency (μ (sd); ms)	State Anxiety μ (sd); max score 33
PDs	Ground	3.816 (4.944)	620.09 (352.415)	8.81 (6.445)] ***
	Threat	4.540 (5.319)	450.13 (337.534)	
OAs	Ground	1.649 (2.240)	409.35 (322.499)	5.05 (3.471)] ***
	Threat	4.680 (4.162)	379.30 (275.194)	

Values are in the form of μ (s.d.). * indicates significance at alpha level 0.017; *** indicates significance at alpha level 0.001.

Initial Conclusions

Firstly, the absence of a significant difference in RelAP between groups indicates that Parkinson's Disease with Freezing of Gait has no effect on the magnitude of response to a visual perturbation, therefore we must reject our hypothesis that people with PD and FOG rely more heavily on visual input than their healthy cohorts. In other words, we cannot conclude from this initial result that the severity of PD symptoms influences sensory reweighting. Further correlation analysis will elucidate the nature of these findings (see below).

While primary analysis did not reveal significant effects on response magnitude, group differences became apparent in response latency. AP Latency was significantly increased in PDs compared to the healthy OAs. This suggests that, while the magnitude of the postural response to the perturbation was similar between groups, the PD group response was delayed compared to the healthy OA group, indicating an impairment in sensory integration in PDs with FOG. This suggests that PD with FOG may influence the time taken to detect a disparity in sensory modalities, concurrent with previous research. For example, Falkenstein and colleagues (2001) found that basal ganglia deficits are linked to error detection in PDs.

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Although all participants did self-report as being significantly more anxious at Threat than Ground, this did not translate to a change in magnitude of response to the perturbation in either Group. This is not necessarily surprising given the effects discussed in the previous chapter regarding a possible ceiling effect, where older participants may already be reacting to such a degree at Ground level that this cannot be further exacerbated by postural threat. Furthermore, we do see a trend of PDs reporting higher anxiety levels than OAs during both conditions. Postural anxiety may be more relevant in the PD group, supporting the idea that PDs (especially those with FOG) experience increased anxiety about falling (fear of falling; FOF) (Adkin, Frank, & Jog, 2003). The significantly increased variance in PDs' RelAP during Threat may point to a significant between-group difference in response magnitude being masked by the response variance in this group.

Prior to more in-depth interpretation, and in order to further elucidate the nature of these results, further analyses on the relationship between FOG scores and postural behaviour were performed on the data from the PD+FOG group.

Correlational Analyses

As we were primarily concerned with whether or not severity of Freezing symptoms have an effect on postural behaviour at baseline, the correlations were performed for data collected at Ground only. Scores representing increased freezing severity were predicted to positively correlate with increased postural response (RelAP and AP Latency). Since the order of conditions was counterbalanced for each participant, it was necessary to ascertain that the order of conditions did not affect postural response magnitude or latency. No effect of trial order was found; see Table 6.

Table 6. Test and significance values of independent samples t-tests comparing trial order groups on amount of change in postural responses between Ground and Threat.

PDs	RelAP	$Z = 1.799; r = 0.375; p = 0.077$
	AP Latency	$t(21) = 1.14; p = 0.267$
OAs	RelAP	$t(21) = 0.43; p = 0.671$
	AP Latency	$t(21) = 1.621; p = 0.120$

Data pertaining to RelAP in the PD group were not normally distributed, therefore a Mann-Whitney U test was used to analyse the difference between trial order groups for this variable.

Subsequently, one-tailed Spearman's correlations were conducted to check for a relationship between RelAP at Ground and participants' scores on the Freezing of Gait questionnaire. FOG score was significantly negatively correlated with RelAP ($r = -0.443, p = 0.022$;

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see Table 7). Appropriate correlations were conducted to check for a relationship between AP Latency at Ground and FOG. There was a trend of FOG score positively correlating with AP Latency ($r = 0.385, p = 0.042$).

Table 7. Correlations between RelAP/AP Latency at Ground and participants' FOG scores.

	Correlations with RelAP	Correlations with AP Latency
FOG	$r = -0.427; p = 0.022^*$	$r = 0.385; p = 0.042$
State Anxiety	$r = 0.409; p = 0.033$	$r = 0.245; p = 0.142$

* indicates significance at alpha level 0.025

Since anxiety is often linked with freezing pathology, we also checked for correlations between postural responses and state anxiety at Ground, using a one-tailed Spearman's rho. This was not significant for AP Latency ($r = 0.245, p = 0.142$), but a trending positive correlation did occur between RelAP and state anxiety ($r = 0.409, p = 0.033$). No significant correlations occurred in the OA group between state anxiety reports and postural measures. To check for any potential mediating factor of anxiety in the correlation between FOG score and postural responses (and vice versa), we performed non-parametric partial correlation analyses. The correlation between FOG score and RelAP became a negative trend when controlling for state anxiety levels ($r = -0.433, p = 0.036$). Meanwhile, the trending positive correlation between FOG and AP Latency became significant when controlling for state anxiety levels ($r = 0.499, p = 0.017$).

Discussion

This study aimed to examine the impact of incongruent visual stimulation in a group likely to experience reduced proprioceptive gain and increased susceptibility to anxiety in comparison to healthy controls, during non-threatening compared to postural threat conditions. This section will first review how the additional correlational analyses elucidate the primary analyses, followed by a discussion of these results as a whole in the context of research on Parkinson's Disease and sensory processing.

The exploratory analyses suggest that those with increased FOG symptoms are more likely to show a delayed response compared to those with less freezing pathology, but that the response itself is potentially of a lesser magnitude. They also suggest that changes in postural response are explained by physiological issues with processing sensory information, rather than anxiety.

The delayed and possibly muted responses with increased FOG severity may be due to increased motor inhibition in those with higher levels of FOG. Georgiades and colleagues (2016)

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demonstrate impaired motor initiation and increased inhibition in PD patients with FOG. Freezers experienced frequent start hesitation and slower footstep initiation, as well as less ability to inhibit movement, compared to non-freezers during a VR motor task. However, these previous findings pertain to impairments in voluntary movements/actions rather than involuntary visually-evoked postural responses. A key symptom of FOG is non-purposeful motor arrests, thought to be at least partly due to pathological subthalamic activity, but the pathogenesis of FOG events remains a subject of debate (Georgiades et al., 2019). For example, Nutt and colleagues (2011) implicate breakdowns in locomotion and balance circuits as neurological underpinnings of FOG, such as impairments in descending control of spinal networks on gait control, and disruptions of the loop(s) between the basal ganglia (BG) and the supplementary motor area (SMA; required for self-generated movement). Such atypical neurological activity and the potential downstream effects on movement abilities may help explain the delays in postural response observed in the PD+FOG group in the current study.

Impaired perceptual processing of the environment is another proposed causal factor of FOG. For example, prior research has found an exaggerated response to action-relevant visual information (such as an upcoming doorway) in those with PD and FOG (Cowie, Limousin, Peters, & Day, 2010). However, this effect does not occur when the patient is seated, so it is unlikely to be a simple visual-perceptual processing deficit – there must be deficits in the complex online planning of locomotor adaptation based on environmental changes. Wang and colleagues (2016) propose that these deficits in visual processing are due to abnormal functional connectivity between the Pedunculopontine Nucleus (PPN) and visual temporal areas, with white matter deficits spreading to motor, sensory, and cognitive regions. In the current study, these impairments in functional connectivity could explain why we observed increased response latency in the PD+FOG group, with the degree of latency escalating in magnitude (along with a trending decrease in response amplitude) with increased severity of FOG. This is an area that warrants further research, perhaps with more emphasis on how these connectivity differences relate to changes in complex online locomotor planning and sensory reweighting.

One possible interpretation of the lack of group difference in response magnitude is that people with PD do not rely any more heavily on vision in any given instant than healthy people. While sensory integration impairment in PDs has been indicated in previous research, these previous findings have usually observed a persistent upweighting of vision in PDs compared to healthy OAs during prolonged or repeated exposure to sensory disparity. The results observed here suggest that, while in the context of prolonged stimulation used in previous studies PDs may persistently rely on vision more than healthy cohorts, they do not necessarily rely more on vision at any *one given*

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moment. In other words, they are unable to suppress inaccurate visual information, but vision is not necessarily constantly upweighted compared to non-diseased older adults. Cowie and colleagues' (2010) finding that people with PD's exacerbated response to visual information only occurs during ongoing motion is perhaps consistent with this concept. However, given the trending negative relationship between FOG severity and response magnitude (which we speculate may be due to disease-related response inhibition), it is arguable that if a non-FOG PD group was compared to healthy OAs in this paradigm, we would then observe a significant difference in response magnitude indicative of the increased visual reliance suggested in previous research. That said, this is an area that warrants further investigation, using a paradigm similar to the current study including both FOG and non-FOG PD groups to compare with healthy OAs.

Limitations

Again, the use of a paradigm that only includes one trial per condition lends itself to very variable responses; this variability has implications for our null results, which, due to the reduction in statistical power, must be considered cautiously. In other words, it is possible that the lack of statistically significant difference in RelAP magnitude between groups is due to a Type 2 error. However, since differences in habituation to a visual perturbation has been observed in these populations (Bronstein et al., 1990), a paradigm using limited perturbations was deemed necessary to avoid the potentially confounding effects of habituation to the visual perturbation and allow for between-group comparisons.

Since the current study did not measure participants' experiences of vection, we cannot reliably dissociate participants' perceptions of sensory disparity from their motor responses to perceived vection. On the other hand, short of neuroimaging, it is unclear how one might disentangle the perceptual and motor aspects of visual self-motion, given that self-reports of perceived self-motion would be unreliable since it may be that their perceptions are functionable – simply delayed. This is an important area to investigate further in future research, using carefully constructed paradigms to attempt to tease apart these mechanisms.

Future Research

Aside from deficits in subcortical and motor areas described above, cognitive/executive function deficits may also explain the latency of responses. Other studies have shown impaired reaction times in motor response in people with PD, where cognitive capacity and frontal lobe function correlated with RT (Jordan, Sagar, & Cooper, 1992). Similarly, poorer frontal lobe function in FOG patients compared to non-FOG patients; Cohen and colleagues (2014) compared PDs with and without FOG in several executive function tasks. FOGs displayed tendency to hesitate and miss

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response window in Go trials of Go-Nogo task and made slower responses in incongruent Stroop task trial compared with non-FOGs. Nutt and colleagues (2011) also describe pre-frontal cortex (PFC) dysfunction as a potential causal factor for FOG, reviewing other studies showing impairment of executive function in FOG, e.g. set-shifting, attention, problem solving, and response inhibition. While none of the participants in the current study reached a threshold for cognitive impairment (Trzepacz et al., 2015), it is possible that more specific tests of executive function may yield observation of significant within-subject differences in postural response in a similar cohort of PD patients. Future studies should endeavour to replicate the current findings using a more thorough battery of neuropsychological/executive function tests and examine how this affects latency of postural response.

Another potential factor influencing the observed behaviours in this study is Conscious Control of Movement (CCM). While increased conscious control does seem to be a factor of healthy ageing (Boisgontier et al., 2013; Chow et al., 2018; Reynolds, 2010), this has the potential to be exacerbated in ageing pathology. In PD, automatic movement is compromised (Wu, Hallett, & Chan, 2015). One aspect of the disease's typical bradykinesia is the loss of motor automaticity, where the ability to perform movements that were previously achievable without conscious thought (such as arm swing during walking; (Nieuwboer et al., 1998) is impaired. This is thought to be due to basal ganglia damage, which impairs the regulation of well-practiced movements (Almeida, Wishart, & Lee, 2003; Garraux et al., 2005; Wu, Hallett, & Chan, 2015). Research by Morris, Iansek, Summers, and Matyas (1995) suggests that reduced movement automaticity may lead to compensatory increased conscious control of movement. People with PD often self-report increased conscious monitoring and control with regards to their movement; Masters, Pall, MacMahon, and Eves (2007) show that people with PD tend to increase their conscious movement control as the disease progresses.

Those with FOG are particularly compromised in motor automaticity (Vandenbossche et al., 2013): freezing episodes often occur during performance of a task simultaneously with another task that is usually automatic, e.g. talking while walking. In PD patients and especially those with FOG, external sensory cues seem to help people who have difficulty self-generating movement because they bypass the supplementary motor area of the brain, which usually enables automatic movement (Ma, Trombly, Tickle-Degnen, & Wagenaar, 2004; Rocha, Porfírio, Ferraz, & Trevisani, 2014). To use a specific example, step initiation is internally generated and more dependent on the BG than when externally generated by stimuli; a loss of automaticity explains why the movement of people with FOG is ameliorated by external cues. For example, using an auditory cue such as a ticking metronome improves the stability and gait pattern of walking in PD patients, because it bypasses the

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deficit in the brain's ability to maintain an internal rhythm and provides a voluntary rhythm (McIntosh, Brown, Rice, & Thaut, 1997). Using a visual cue enables the visual-cerebellar motor, facilitating an improved gait pattern (Azulay et al., 1999). Similarly, external somatosensory cues have been shown to aid PD patients with FOG with movement, such as using vibratory stimuli on the legs to help with walking. This presumably compensates for the loss of reliable proprioceptive signals in PD (Konczak et al., 2009). This concept of conscious motor processing warrants further exploration with regards to sensory reweighting; it would be informative to isolate this factor in a further study to see if increased CMP affects reliance on vision during a simple standing task.

Concluding Remarks

Overall, there are clearly some disease-related differences in sensory processing/how the brain deals with incongruent senses, supporting previous research. However, our study suggests that these differences may be more nuanced than previously implied.

Based on the lack of between-group differences in response magnitude, it is possible that people with PD may not rely on vision more than healthy OAs in any given moment, despite inability to suppress visual information given ongoing disparity. However, since our study only recruited PD patients with FOG, we cannot reliably generalise this concept to the wider PD population. Further work is necessary to explore this possibility in PD patients who do not experience any FOG symptoms, preferably using a paradigm that controls for possible habituation effects while also mitigating against the low power that comes with using limited perturbations. That said, within the PD group, those with increased FOG symptoms showed differences in visual weighting to those who experience FOG symptoms to a lesser degree, with a postural response characterised by a delayed and possibly muted response to optic flow. This suggests that a lower magnitude of postural response could be possibly due to motor inhibition mechanisms observed in people with FOG, potentially caused by impairments in sensory processing networks and connections between the basal ganglia and motor areas important for self-initiated movement.

It is clear that further work is necessary to evaluate the behavioural consequences of changes related to neurodegenerative disease and to explore the potential range of factors that might influence sensory reweighting in the PD population, especially those with FOG. While the current results do provide limited evidence that the sensory integration of people with Parkinson's Disease and Freezing of Gait is more affected by a visual perturbation than their healthy counterparts, more robust research strategies are required to more fully elucidate this particular research area.

Chapter 5.**Study 3: The Effect of Increased Conscious Motor Control on Orthostatic Postural Control Responses to a Visual Perturbation**

Balance control involves the coordination of multiple sensory systems, integrating visual, vestibular, and proprioceptive inputs (Della-Justina et al., 2015; Peterka, R. J., 2002). Typically, the central nervous system (CNS) weights these sources in respect to their perceived reliability, and integrates them accordingly to maintain stable balance (Bronstein, 2019; Della-Justina et al., 2015; Peterka, R. J., 2002). However, different factors influence the way these senses operate. For example, increased postural threat (typically induced via standing participants on a raised platform) leads to both greater subjective feelings of anxiety and increased gain in vestibular and muscular signals (Cleworth et al., 2016; Horslen et al., 2013; Horslen et al., 2014).

In Chapter 3, young and older adults were exposed to one high and one low postural threat condition, accompanied by a single visual perturbation in each condition. Both younger adults (YAs) and older adults (OAs) showed an increased anterior centre of pressure (COP) displacement in reaction to a pitch-up visual perturbation when placed at height compared to at ground level. Both groups showed further differences in several other related parameters such as the response latency, and the velocity of movement between perturbation onset and anterior peak. We interpreted this augmented postural response as evidence of increased reliance on visual information, most likely driven by the concomitant significant increase in state anxiety. The study also supported previous research by demonstrating that OAs are more reliant on visual input in general, and less tolerant of sensory disparity (Alberts et al., 2019; Jeka et al., 2010; Ramkhalawansingh et al., 2016). The OAs showed significantly increased COP displacement measures both at ground and at height level compared to their younger cohorts. Their levels of anxiety, however, were not significantly different than those of the younger group, and at height the levels of anxiety were only significantly correlated with postural response in OAs. The fact that the levels of anxiety between the groups were comparable, yet OAs still displayed an increased postural response to the visual perturbation, suggests that mechanisms other than anxiety also influence the degree to which vision is used to maintain stable posture.

One possible explanation for the findings in Chapter 3 relates to the degree to which an individual directs attention internally towards monitoring or controlling their balance movements. OAs show an increased tendency to consciously control their balance movements (Boisgontier et al., 2013; Chow et al., 2018; Clark, 2015; Magnard et al., 2019), particularly those at higher risk of falling (Ellmers, Cocks, & Young, 2019a; Uiga et al., 2018; Wong et al., 2008; Young & Williams, 2015).

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Furthermore, postural threat (induced via a raised platform) appears to increase conscious control of balance-related movement processes in both YAs (Ellmers & Young, 2018; Huffman, Horslen, Carpenter, & Adkin, 2009; Zaback, M. et al., 2016) and OAs (Ellmers et al., 2019a; Johnson, Zaback, Tokuno, Carpenter, & Adkin, 2019). Postural threat manipulations have also been shown to lead to an increase in sensory gain (Cleworth et al., 2016; Cleworth et al., 2019). Cleworth and colleagues (2019) placed YAs in two height conditions (low = 1.1m and away from edge; high = 3.2m) and delivered continuous roll platform rotations, and instructed them to indicate their perceived amplitude of medio-lateral body movements using a handheld encoder, while also collecting kinematic data. While the actual level of sway amplitude remained comparable across conditions, perceived sway amplitude, along with self-reported and physiological levels of anxiety, was significantly increased for the high height condition. The authors proposed that such change may be underpinned by participants directing preferential attention towards threatening stimuli and the subsequent amplification of sensory processing related to the perception of self-movement. Thus, in conditions of heightened anxiety, the manner in which relevant senses are processed and perceived is altered. Specifically, increased anxiety appears to heighten the sensitivity of balance-relevant sensory systems and amplify the perception of whole-body movement. This could be the result of increases in attention toward own-body movement (Ellmers, Kal, & Young, 2020).

Further inference that increased conscious movement control and visual input are interrelated may be taken from a study by Schniepp et al. (2014), who found that patients with Phobic Postural Vertigo show increased conscious control of movement as well as a shift towards visual control of movement as opposed to proprioceptive. It is, therefore, possible that our previous findings (increased visual reliance both during conditions of postural threat, and in older adults compared to younger) may be underpinned by greater conscious processing of balance movements. In Chapter 4, we exposed OAs with Parkinson's Disease (PD) and Freezing of Gait (FOG) and healthy age-matched controls to the same paradigm and measured their postural responses. We found that while the amplitude of the postural response was comparable to the healthy age matched controls, those with PD/FOG showed increased latency of response compared to their healthy counterparts, with FOG severity positively correlating with degree of latency. Prior research has identified increased conscious control of movement (CCM) as a common factor of PD (Masters et al., 2007). Given the association between PD and lack of motor automaticity and the need for conscious motor control (Masters et al., 2007; Morris et al., 1995; Nutt et al., 2011), we might consider PD as a model for increased requirements for CCM. However, when comparing the data indicating the degree of visual reliance, the null result between PD and non-PD groups in Chapter 4 indicates that CCM may not be a primary driver of increased weighting on visual input. Nevertheless, this model of PD has

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several confounds, as PD affects several other factors associated with sensory integration, such as processing of vestibular (Bertolini, Wicki, Baumann, Straumann, & Palla, 2015) and proprioceptive input (Konczak et al., 2009). Therefore, since the results from Chapter 4 cannot give a definitive answer on whether or not increased need for conscious control of movement is a contributing factor to increased reliance on vision, it is necessary to carry out a study that isolates and manipulates conscious control of movement to answer the research question of whether or not this factor leads to increased visual reliance.

While Cleworth and colleagues (2016) postulate that changes in sensory processing are due to threat-related increases in attention towards own-body movements, it is possible that these factors operate independently. In Chapter 3, for example, the OAs may have experienced increased reliance on vision compared to YAs due to their increased tendency towards conscious control of movement – despite comparable levels of anxiety. Studies using directed focus instructions demonstrate pronounced behavioural changes when using internal focus instructions, such as less efficient gait (Mak, Young, Lam, Tse, & Wong, 2019) and more constricted visual search behaviour (Ellmers & Young, 2019). One possible mechanism is that increased CCM may drive increased reliance on vision through inducing the senses to be more aware of potentially destabilising stimuli in the environment, thus increasing the weighting of visual input for balance control. So far, no studies have looked to experimentally increase CCM while measuring visual reliance. Given the lack of research exploring causal effects of attentional focus/CCM on sensory reweighting, questions remain over how and to what extent the effect of postural threat on sensory reweighting is moderated by attentional focus.

The current study aims to explore this possibility by experimentally manipulating the level of CCM in YAs and examine postural reactions to a visual perturbation as well as emotional reactions to postural threat. We hypothesised that increasing participants' focus on internal movement processes would elicit an increased reliance on vision to regulate postural stability compared to Baseline. This would be evidenced by greater magnitude of anterior-posterior COP displacement measures in reaction to a visual perturbation, as observed previously in YAs during postural threat and in OAs during both threatening and non-threatening environments (Chapter 3). We expected this difference to be present during a low-threat condition (Ground level), but not necessarily during the Threat condition (standing on an elevated platform), since we expect that postural threat may lead to involuntarily increased conscious control of movement irrespective of an internal focus experimental manipulation.

Materials & Methods

Participants

A new cohort of 31 YAs (18-36 years old, $\mu = 24.48$, s.d. = 3.81), were recruited from undergraduate and postgraduate courses at Brunel University London. All participants had normal or corrected-to-normal vision, and no diagnosed musculoskeletal or neurological disorders. Those participants using vision-correcting equipment (e.g. glasses, contact lenses) wore them in the VR environment. All participants provided written and informed consent following approval obtained by the Brunel University London ethics committee. The research protocol was carried out in accordance with the principles laid down by the Declaration of Helsinki.

Equipment

The equipment and VR environments were identical to that used in Chapters 3 and 4, with a Threat and Ground environment/condition (see Figure 12, Figure 13). COP data were recorded at 1000Hz using a Kistler Forceplate (Kistler 9287BA), with feet positioned hip-width apart on the forceplate. Participants' toes were aligned to a marked line to maintain foot position consistency between both participants and experimental trials. The anterior edge of the forceplate corresponded to the anterior edge of the VR platform. Forceplate data were synchronised using an analogue channel containing a voltage change triggered by the start of each VR animation/perturbation.

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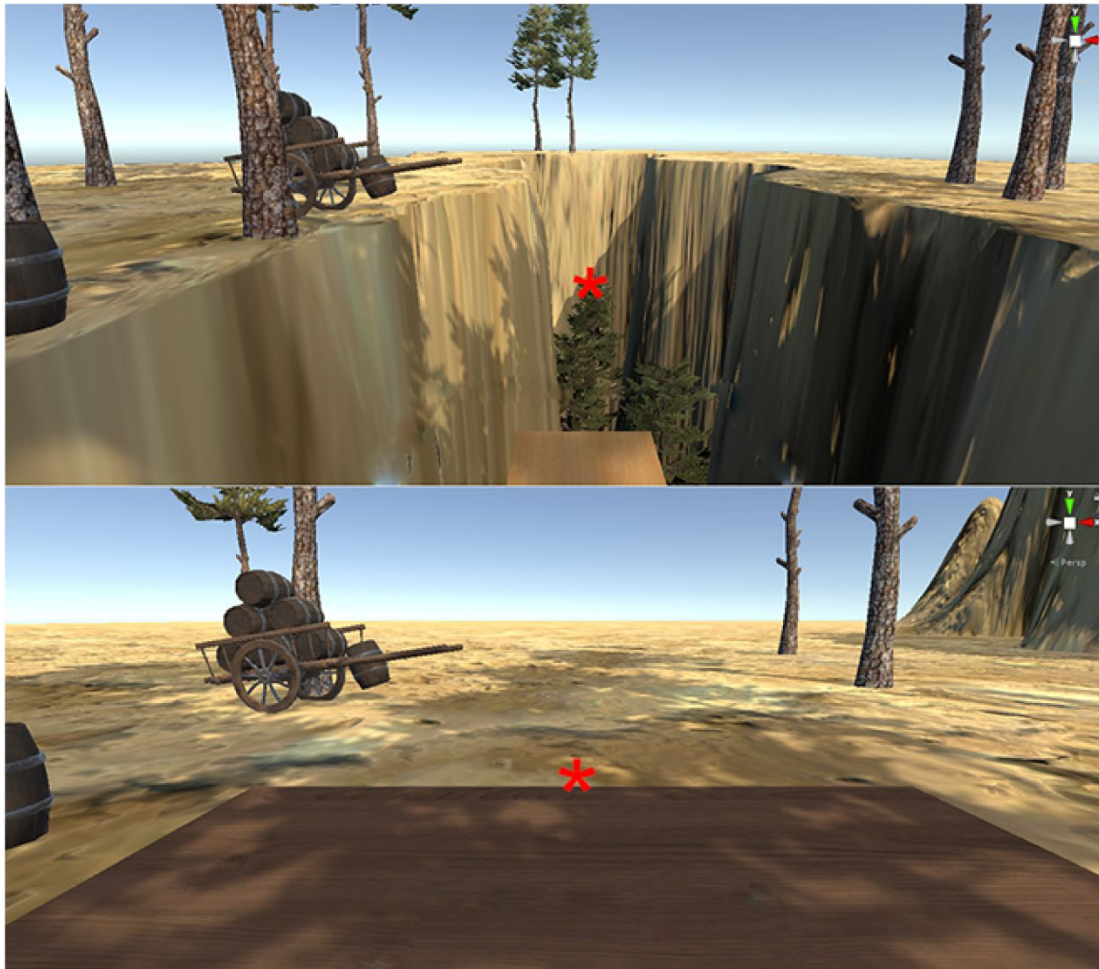


Figure 12. First person view of the Threat condition (top) and Baseline condition (bottom).



Figure 13. First person view of the Threat condition looking down into the gully.

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Procedure

Both the Ground and Threat environments were repeated twice, under 1) a Baseline condition and 2) an Internal Focus (IF) condition. Participants were asked to keep their eyes fixed on a fixation point (positioned at eye level), and either keep all their focus on it and report when it changed colour (Baseline condition), or keep all of their focus on their lower limbs and to report where they felt their weight was distributed (e.g. more on one side, balls of the feet, heels, etc.) at the timepoint when the fixation point changed colour (IF condition). Each of the four experimental trials included one single visual perturbation that occurred at a random timepoint between sixty and seventy seconds following the start of the trial (see Chapter 3 for details of the perturbation), followed by the fixation point changing colour at a point between 3 and 10 seconds after the perturbation (randomised for each participant). The perturbation always occurred prior to the fixation point changing colour to prevent any interference of the colour change/the act of giving a verbal response on their postural response to the perturbation. As detailed in Chapter 3, trials were limited to a single trial per condition to prevent potential sensory re-weighting effects and desensitisation to the VR environment (Bronstein, 1986; Bronstein, 2019; Nishiike et al., 2013; Oude Nijhuis et al., 2009; Pavol et al., 2004). The order of the four trials was randomised for each participant. After each trial, while still in the VR environment, participants completed both the mental readiness form (MRF) (Krane, 1994) as a measure of self-reported state anxiety, and a self-report measure of conscious control of movement (CCM), a shortened version of the Movement Specific Reinvestment Scale (M-MSRS) (Ellmers & Young, 2018). The MRF uses three questions regarding feelings of worry (cognitive anxiety), body tension (somatic anxiety), and confidence, to which the participant must respond on a scale of 1 to 11 (e.g. “On a scale of 1 to 11, how worried are you feeling?”; 1 = not at all; 11 = very much so)⁴. In this study, the three scores are summed to give a total out of 33, with higher scores reflecting greater state anxiety. The M-MSRS uses four items, split into two subscales measuring conscious motor processing (CMP; e.g. “I am always trying to think about my movements when I am doing this task”) and movement self-consciousness (MSC; e.g. “I am concerned about my style of moving when I am doing this task”), each rated on a 6-point Likert scale (1 = strongly disagree; 6 = strongly agree). Participants’ sum of scores for both of the sub-scales on the M-MSRS were calculated, giving a maximum CCM score out of 12 for each subscale; where higher scores reflect greater CCM.

⁴ Note, the confidence subscale was reverse coded.

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Analysis

As in Chapters 3 and 4, characteristics of participants' COP displacement following visual perturbation were evaluated by filtering the raw force data (using a second-order low-pass Butterworth filter with a cut-off frequency of 5 Hz) in MATLAB (R2017a, The Mathworks, Inc.) followed by selecting data from a one second time window starting at perturbation onset. The relative anterior peak (RelAP) was calculated as the value of each participant's mean position during the three seconds prior to perturbation onset subtracted from the position of the anterior peak occurring within the first 1000ms following perturbation onset. This measure served as the primary outcome measure of participants' initial counteractive reaction to the visual perturbation. AP Latency was again also calculated to further elucidate the nature of the postural response by describing the time taken to respond to the perturbation (number of milliseconds between perturbation onset and subsequent anterior peak; see previous chapters for more detailed explanation of these measures).

Statistics

For each case where data were non-normally distributed, we attempted to log transform. Where data became normal, the log transformed data were entered into an appropriate ANOVA with Bonferroni correction. Where data remained non-normal after log transformation, we used non-parametric tests on the original data, which tested for differences between conditions. Any outliers/participants with z-scores over 3 (or less than -3) for any measure were removed from analysis of that measure.

MRF data were not normally-distributed and were not made normal following log-transformation. Therefore, non-parametric tests were used to compare results between groups and conditions. Two outlying participants were removed from analysis, and another was removed due to a technical fault in saving the data. The conscious control of movement data were only normally distributed in Baseline Ground and Internal Threat trials, therefore a mix of appropriate parametric and non-parametric analyses were performed to gauge effects of condition on these scores. The movement self-consciousness scores were non-normally distributed and remained so after log transformation, therefore non-parametric tests were performed on the original data to examine for differences between conditions⁵. Two participants were removed from this analysis due to confusion with regards to completing the M-MSRS questionnaires.

⁵ Where any data remained non-normal following attempted log transformation, non-parametric tests were performed on the original data, to test for differences between conditions.

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RelAP data were not normally-distributed, but became so following log transformation and adding a constant to each value to allow for log-transformation of negative values, therefore were analysed using a mixed ANOVA. AP Latency data were not normally-distributed for either group; log transforming was unsuccessful, therefore appropriate non-parametric tests were used to analyse differences between conditions and groups.

Results

Anxiety

A Friedman test revealed a significant difference between the four conditions (Ground-Baseline, Ground-Internal Focus, Threat-Baseline, and Threat-Internal Focus; $\chi^2(3) = 35.466$, $p < 0.001$). Further non-parametric analysis revealed that there was no significant difference in self-reported anxiety between Baseline and IF trials at Ground ($p = 0.052$; $Z = 1.942$; $r = 0.359$), nor at Threat ($p = 0.192$; $Z = 1.303$; $r = 0.251$), but there was a significant difference between Ground and Threat trials during both Baseline ($p < 0.001$, $Z = 4.018$, $r = 0.773$) and IF conditions ($p < 0.001$, $Z = 3.735$, $r = 0.719$).

Conscious Control of Movement

A Friedman test revealed a significant effect of condition on CMP ($\chi^2(3) = 14.283$, $p = 0.003$). Further Wilcoxon Signed-Rank tests revealed significantly higher scores for CMP measures in the IF condition compared to Baseline at Ground ($p = 0.003$; $Z = 2.928$; $r = 0.553$). A paired samples t-test also revealed a significant difference between IF and Baseline CMP during Threat ($t(28) = 2.182$, $p = 0.038$). CMP did not differ significantly between Ground and Threat during Baseline trials ($p = 0.121$, $Z = 1.549$, $r = 0.293$), nor Internal Focus trials ($p = 0.890$, $Z = 0.138$, $r = 0.026$).

A Friedman test revealed no significant main effects of condition on MSC, therefore no further analyses were carried out for this variable ($\chi^2(3) = 6.431$, $p = 0.092$).

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Table 8. Means and standard deviations of self-reported anxiety and conscious movement processing scores.

	Baseline		Internal Focus	
	Ground	Threat	Ground	Threat
State Anxiety (MRF) (max. score = 33)	$\mu = 5.37$ s.d. = 2.29	$\mu = 10.33$ s.d. = 5.17	$\mu = 6.70$ s.d. = 2.92	$\mu = 11.78$ s.d. = 6.05
M-MSRS – Conscious Control of Movement (max. score = 12)	$\mu = 6.89$ s.d. = 2.57	$\mu = 7.48$ s.d. = 2.13	$\mu = 8.90$ s.d. = 2.40	$\mu = 8.83$ s.d. = 2.45
M-MSRS – Movement Self-Consciousness (max. score = 12)	$\mu = 4.57$ s.d. = 2.65	$\mu = 4.86$ s.d. = 2.52	$\mu = 5.59$ s.d. = 2.89	$\mu = 5.76$ s.d. = 2.76

* indicates significance at alpha level 0.05; ** indicates significance at alpha level 0.01;

*** indicates significance at alpha level 0.001.

Combined, these results act as manipulation checks that confirm that the CCM and State Anxiety manipulations were successful. The M-MSRS results also provide evidence that any increase in participants' CCM was due to the experimental manipulation, rather than the perturbation, since these scores were only significantly elevated in the Baseline conditions.

RelAP (Relative Anterior Peak)

A repeated measures ANOVA revealed no significant effects of either Threat ($F(28) = 0.112$, $p = 0.741$, $\eta_p^2 = 0.004$) or Focus condition ($F(28) = 2.31$, $p = 0.140$, $\eta_p^2 = 0.076$) on the size of participants' RelAP following onset of perturbation. No interaction was observed ($F(28) = 0.508$, $p = 0.482$, $\eta_p^2 = 0.018$).

AP Latency

Wilcoxon Signed-Rank tests did not reveal any significant difference in response latency neither between Internal and Baseline conditions at Ground ($p = 0.510$, $Z = 0.660$, $r = 0.121$) nor at Threat ($p = 0.797$, $Z = 0.257$, $r = 0.047$). There were also no apparent differences when comparing

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Ground and Threat conditions during either Internal Focus ($p = 0.131$, $Z = 1.512$, $r = 0.276$) or Baseline ($p = 0.275$, $Z = 1.092$, $r = 0.199$).

Table 9. Means and standard deviations of anterior-posterior COP displacement parameters.

	Baseline		Internal Focus	
	Ground	Threat	Ground	Threat
RelAP (non-transformed data, mm)	$\mu = 1.225$ s.d. = 2.534	$\mu = 1.109$ s.d. = 1.954	$\mu = 1.416$ s.d. = 1.839	$\mu = 1.816$ s.d. = 3.185
AP Latency (ms)	$\mu = 418.13$ s.d. = 342.708	$\mu = 526.83$ s.d. = 369.861	$\mu = 364.47$ s.d. = 350.931	$\mu = 513.67$ s.d. = 376.494

Discussion

This study investigated whether changes in conscious control of movement may underpin the previously observed relationship between postural threat and increased reliance on visual information (Chapter 3). Specifically, we explored whether instructing participants to direct their focus internally towards consciously processing their balance movements would elicit increased magnitude of balance-related responses to a visual perturbation at ground level, comparable to that previously observed under conditions of heightened threat. This discussion will first discuss the lack of significant effect of conscious control of movement on visual reliance, followed by contextualisation of these findings to previous observations of balance performance.

Part 1. Discussing lack of effect of conscious control of movement on visual reliance

Overall, there is no observable significant effect of increased Internal Focus (and subsequent increased CCM) on postural response to a visual perturbation, therefore we must reject our hypothesis that increased conscious motor control elicits an increased reliance on visual information for orthostatic balance.

One possibility is that CCM simply does not increase reliance on vision. Previous observations indicate that populations such as older adults and those with Parkinson's Disease do rely more on vision while also demonstrating increased CCM. However, this age- and/or disease-related increase in CCM may not be a driving factor of increased visual reweighting, but rather a

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consequence of it. It is possible that when CCM alone is increased, attention is directed towards one's own body, and lessens the awareness of external visual stimuli (though not of a sufficient magnitude to cause a significant decrease in postural response).

Alternatively, it might be that CCM only increases visual reliance when one can see one's own body movements. The full version of the MSRS (i.e. the extended version of the mini-MSRS that was used in the present study), which sees score increases in PDs and many OAs, involves statements such as "If I see my reflection in a shop window, I will examine my movements" (Masters, Eves, & Maxwell, 2005). High agreement with this statement presumably indicates higher visual awareness of one's own body. In contexts of impaired proprioception such as PD, this is predictable, since successful movement presumably relies more on the relatively unimpaired sense of vision (Bronstein et al., 1990; Bronstein, 2019; Butler et al., 2010; Knill & Pouget, 2004). In the current study, people were not able to see their own body in VR. This suggests that if CCM does indeed increase visual reliance, it is related to visual feedback of one's own body movement rather than just an internal awareness. Future studies examining internal focus and sensory reweighting in VR should include visual feedback of body movement, perhaps using an avatar. Since this data was collected, some virtual reality games have developed the ability to include reliable avatar body feedback that matches the player's movements, especially in the upper half of the body. The new Valve Index can even reliably replicate individual finger movements. In some new videogames, whole body avatars are available in VR. This is probably not sufficiently refined for reliable visual feedback of movement for research involving gait analysis, but it is perhaps good enough for studies on orthostatic balance. Future studies could also combine motion capture with VR to feedback participants' body motion to the VR system and replicate the participant's movements in real-time in a VR avatar.

Part 2. Contextualising these findings to previous observations of balance performance

The current results suggest that an increase in conscious control of movement does not affect visual reweighting for balance control. Previous research has observed that promoting reduced conscious control of movement, or directing attention towards external cues, improves control of balance (e.g., studies on balance learning). Wulf, McNevin, and Shea (2001) demonstrated a reduction in balance errors when participants were asked to adopt an external focus of attention during a dynamic balance task compared to an internal focus. Similarly, Chiviacowsky, Wulf, and Wally (2010) showed improved balance performance in a group instructed to perform a task using external focus compared to the group that received internal focus instructions. Following this work, Wulf (2013), in her review of focus on attention and motor learning, concluded that inducing

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external focus produces balance performance benefits across various tasks, age groups, and skill levels.

Given these previous findings, clearly attentional focus has an influence on balance control. However, the lack of effect of Focus on visual reliance in the current study suggests that these previously observed balance changes are unlikely to be a result of focus-induced changes in visual reliance. Therefore, manipulations of direction of focus must induce changes in mechanisms other than visual weighting, such as proprioceptive and/or vestibular weighting. Richer and Lajoie (2020) instructed participants to remain standing while either focussing neutrally, internally, externally, or while performing easy or difficult cognitive tasks. Centre of Pressure data indicated that participants' stability improved and became more automatic in the external focus and cognitive task conditions, with increased input from higher frequency bands suggesting greater input from the vestibular system during tasks that promoted greater automaticity. Thus, decreased conscious movement control is associated with increased vestibular input. Reynolds (2010) found vestibular-evoked sway responses were attenuated by conscious control of standing balance (at least for the later component of the sway response), again indicating that conscious control of movement affects vestibular processing by reducing vestibular reliance. We might expect that directing attention internally would decrease vestibular input, thereby possibly increasing the response to a visual stimulus since vestibular gain is decreased (and therefore downweighted). Nevertheless, we did not observe such an increased response to visual stimulation in the current study. Since CCM and proprioception are linked (Gottwald, Owen, & McNevin, 2020), we cannot assume changes in vestibular function will influence visual weighting, since this process of vestibular input weighting change might simply reflect a trade-off between proprioceptive and vestibular inputs. However, Reynolds (2010) also suggests that voluntary control of movement reduces the threshold for detecting sensory conflict, so any incongruent stimulus would be attenuated. This could be why we do not observe a difference between internal and baseline conditions in the current study, since it is possible that the visual stimulus was detected earlier and the response thus attenuated.

Other researchers have found no effect of direction of attention on balance control. de Melker Worms and colleagues performed two studies in 2017 (de Melker Worms et al., 2017; de Melker Worms, Stins, van Wegen, Loram, & Beek, 2017) showing no effect of external versus internal focus instructions on balance control in elderly adults during a five-minute gait task. While it is arguable that their null findings may be due to participants being unable to maintain internal focus for that length of time, these results are in line with our finding that internal focus does not influence visual weighting. At least, they demonstrate that the improvements in balance

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performance with external focus may be restricted to orthostatic/simple balance tasks and are not generalisable to more complex gait tasks.

Limitations

The absence of a significant effect of Threat on participants' postural responses contrasts with our findings in Chapter 3, where we observed significantly increased postural response to a visual perturbation in the Threat environment compared to the Ground environment. One issue in the current study is that despite only using a single perturbation in each condition and counterbalancing the trials, the four sequential conditions may have been sufficient enough for the CNS to begin downweighting visual signals due to the repeated incongruence with non-visual sensory inputs (Bronstein, 2019), despite significant increases in self-reported CCM and anxiety. Therefore, it is a possibility that due to the repeated trials and potential subsequent habituation to the perturbation, any effects of Internal Focus and/or Threat are being "washed out" resulting in a Type 2 error; consequently, the null results of this study must be considered with caution. Including a "buffer" task between trials in future experiments might lead to a reweighting of sensory inputs to normal levels, thus "resetting" the balance of visual and non-visual inputs and allowing for more valid measurements of the effects of increased internal focus on visual reliance.

The current paradigm was essentially attempting to mimic in YAs the tendency of OAs to consciously control their movements. However, as discussed above, presumably CCM in OAs develops relatively gradually as they age as a learned adaptation – indeed, Mak, Young, Lam, Tse, and Wong (2019) note that the manipulations of focus on own-body movement in the laboratory are unlikely to reflect the specific conscious motor processing mechanisms in OAs. In YAs, asking them to suddenly switch to an unfamiliar state of attention/method of standing still may not be a valid method of recreating the CCM prevalent in OAs and people with PD. In other words, it is possible that this gradual learned adaptation to increased CCM may be a factor in increasing visual reliance in OAs, but a sudden switch in attention direction in YAs does not have the same effect on sensory reweighting, despite the self-reported rise in conscious control of movement.

Conclusions

Based on the current results, we cannot conclude that experimentally manipulated conscious control of movement has any observable effect on visual reliance. This may be due to several factors, such as the lack of visual feedback of participants' own-body movement, which has previously been demonstrated to have an effect on balance control. Alternatively, the null results could be due to the nature of the task, which required young adults to control their balance in a way that is unnatural for them, compared to it being a naturally occurring learned adaptation in older

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adults. In sum, it is still unclear to what degree internal focus of attention affects balance control in general. If it does, our results suggest it may not affect visual reweighting – rather other mechanisms involved in balance such as vestibular reweighting. These possibilities warrant further investigation in future studies. Furthermore, this study serves to reiterate the importance of restricting the number of consecutive trials where incongruent sensory stimulations are used, since this may be resulting in downweighting of vision, despite sustained increases in self-reported measures.

Chapter 6. General Discussion

Overview of Thesis

The previous five chapters can be described as an attempt to further illustrate the effects of postural threat on visual reweighting for balance control, in an effort to better understand how changes in sensory weighting affect ageing and clinical populations, and how we might be able to mitigate fall risks in future.

The first experimental chapter (Chapter 3) aimed to explore how postural threat affects the reweighting of sensory inputs, particularly whether it increases reliance on visual information, and how this is affected by ageing. Younger (YAs) and Older Adults (OAs) were exposed to a small pitch-up visual perturbation in two virtual environments, one designed to emulate postural threat and the other non-threatening. Both groups demonstrated an increased response to the visual perturbation during the Threat condition, indicating an increase in reliance on vision with anxiety. Meanwhile, the OAs showed an increased overall response compared to the YAs, indicating the involvement of factors other than anxiety in increasing visual reliance. The second study (Chapter 4) aimed to investigate the impact of Parkinson's Disease on reliance on vision. This study compared a group of people with Parkinson's Disease and Freezing of Gait (PD+FOG) – a disease that affects proprioceptive sensory input and increases the need for conscious control of movement – with healthy controls, during both threatening and non-threatening environments. The results of this study were less clear; while there was a clear difference between the two groups in the timing of their postural response to the perturbation, the magnitude of the postural response was comparable between groups in both conditions. However, relationships between the severity of FOG symptoms and postural response characteristics were observed, with more severe FOG being linked with more delayed postural responses of a lesser magnitude. The third study (Chapter 5) aimed to evaluate the causal links between conscious motor control and visual dependence in a more direct manner, by exploring how increased conscious control of movement (CCM⁶) might impact visual dependency as a moderator of postural threat, as a potential explainer for the age group difference observed in the first study. YAs were placed in a non-threatening virtual environment and instructed to direct their attention either internally towards their own body movement, or towards an external stimulus, while again, as in previous chapters, experiencing a visual perturbation. Results implied that increased CCM does not significantly increase reliance on visual information, which

⁶ In this chapter, IF refers to the specific condition used in Chapter 4's paradigm (where participants were indirectly instructed to increase their Internal Focus), whereas CCM refers to the general concept of increased conscious movement control discussed in the wider research field.

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suggests that the previously described age group difference is due to age-related factors other than increased internal focus (IF, or conscious control of movement) in older people.

Main Findings

Analysing the results of these studies reveals several noteworthy points. First, we do see an effect of increased anxiety on the response to a visual perturbation, particularly in young people: the study in Chapter 3 shows increased visual reliance in conditions of heightened perceived postural threat that induced anxiety. Thus, we do see that anxiety leads to upweighting of visual input – which could possibly be interpreted with respect to an Attentional Control Theory (ACT)-type model (Eysenck, Derakshan, Santos, & Calvo, 2007). This model proposes that anxiety causes increased salience of threat-related stimuli – in the case of the present set of studies, the visual environment. This could underlie the findings in Chapter 3, where participants may have been hyper-vigilantly attending to the visual environment at Threat due to being more anxious, thus more sensitive to changes in visual scene motion, resulting in increased visually-evoked postural responses (VEPRs) at Threat compared to Ground. This model is also particularly relevant for OAs, especially those with Fear of Falling (FOF), who show increased likelihood to direct attention towards threat-relevant stimuli (Brown, White, Doan, & de Bruin, 2011). However, since ACT proposes that this increased threat-related attention is induced by anxiety, and there were no discernible differences in anxiety levels between groups, it is unlikely that this model can fully explain the main group effect in these findings observed in Chapter 3.

Regarding the impact of neurodegenerative disease on visual control of posture, the only significant Group effect in Chapter 4 was that the PD+FOG group took longer to react to the perturbation than healthy OAs. This may be representative of disease-related bradyphrenia and/or impairments in detection of sensory errors (Falkenstein et al., 2001; Rogers, 1986; Steinke, Lange, Seer, Hendel, & Kopp, 2020), but the lack of clear observable group differences in the magnitude of postural response indicate the necessity for further, more directed research on if, and how, sensory reweighting is affected in people with PD, particularly those with FOG. The further analysis of the relationship between self-reported measures and postural responses in the PD+FOG group indicated that the degree of FOG severity is linked to a more delayed and potentially attenuated reaction to visual information that is incongruent with non-visual sensory input, indicating that FOG symptoms increase with impairments in processing sensory discrepancy. The analyses also indicated that these changes in postural response were independent from anxiety levels, implicating other sensory processing differences in sensory reweighting in this group.

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As mentioned above, the results of Chapter 5, a study including an IF condition aimed at increasing participants' CCM, suggest that IF/CCM is not a potential driving factor for these observed differences in postural response. Several studies provide evidence that anxiety leads to increased CCM (Ellmers et al., 2019b; Huffman et al., 2009; Johnson et al., 2019; Zaback, M. et al., 2016; Zaback, Martin, Adkin, & Carpenter, 2019), but the current results imply that CCM does not have an effect on visual weighting – at least not in this context of orthostatic balance. Likewise, other studies have found that directing attention away from own-body movement and/or towards external stimuli improves balance control (Chiviacowsky et al., 2010; Wuehr, Brandt, & Schniepp, 2017; Wulf et al., 2001; Wulf, 2013), but again our results from Chapter 5 would suggest that this is due to changes in mechanisms other than visual weighting, such as vestibular and/or proprioceptive processing (Reynolds, 2010; Richer & Lajoie, 2020).

More recent work may offer some theoretical resolution to these conflicting findings – some suggest that increased postural responses at Threat, specifically increased sensitivity to afferent feedback, are due to increased CCM (Wuehr et al., 2017; Zaback, Martin et al., 2019). However, Ellmers, Kal, and Young (2020) found that that this still occurs even when participants are not experiencing increased CCM. Participants were placed at Ground and Threat, with either no distraction task (baseline), or a distraction task to divert attention from conscious motor processing. Their participants showed a shorter transition window between open and closed loop postural control (indicative of a lower threshold for sensory feedback) at Threat – during both the non-distraction and, importantly, the distraction task. They also found coinciding increases in both sway frequency and sample entropy, reflecting higher automaticity, at Threat compared to Baseline. LeDoux and Pine (2016) describe two types of anxiety responses – automatic and conscious, which may differentially affect postural responses to Threat. Therefore, as Ellmers et al. (2020) argue, the increased postural response at Threat probably relates more to automatic mechanisms triggered by the Central Nervous System (CNS). This response may then be constrained by the conscious processes that then 'kick in' due to the conscious experience of anxiety. Thus, a lack of effect of Internal Focus in Chapter 5 could be because the process of visual reliance/upweighting is an automatic, defensive reaction, independent from a conscious emotional reaction. According to LeDoux and Pine (2016), the experience of being at Threat would have increased participants' physiological sensitivity to threatening inputs (in this case, the visual perturbation), resulting in an automatic postural response to the perturbation – separate from the emotional/cognitive response. Thus, we see an increase in postural response to the perturbation during the Threat condition compared to Ground in Chapter 3, but no difference in postural response between Internal Focus/Baseline tasks in Chapter 5 since these changes in CCM may reflect separate, more cognitive

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processes. However, this does not explain why we do not see a main effect of Threat on postural response in Chapter 5. This may be due to habituation effects caused by using four perturbations/trials (compared to only two trials included in Chapters 3 and 4), therefore future work using more carefully constructed paradigms is necessary to further explore the possibilities of how CCM affects postural control, and how it interacts with experiences of heightened anxiety. For example, future research could implement paradigms including “buffer trials” to prevent habituation to the visual disparity.

Implications of Individual Measures

By defining the various outcome measures used in this thesis, we can attempt to explain the mechanisms involved in driving the observed relevant behaviour. Relative Anterior Peak (RelAP), as already described in earlier chapters, may be considered an initial compensatory response to the visual experience of a pitch-up perturbation. Anterior Peak Latency (AP Latency), measured as the amount of time between perturbation onset and when the participant’s subsequent anterior movement reaches a peak, represents the time it takes participants to respond to the visual perturbation.

In the second study, participants with PD+FOG seem to show few differences compared to their healthy cohorts, but disease-related changes in response latency appear to be attenuated. Diseases such as PD+FOG may not have much effect on the actual magnitude of response to sensory incongruence, which seems to be indistinguishable from adults of the same age, but they may affect the time taken to perceive and react to the incongruency. Again, this could be due to sensory processing deficiencies in neurodegenerative diseases such as PD (Falkenstein et al., 2001; Rogers, 1986; Steinke et al., 2020). It is possible that disease-related deficiency in dopamine affects the detection of sensory errors (e.g. impaired performance in tasks requiring high cognitive control such as a Go-NoGo task (Falkenstein et al., 2001)) – possibly due to the fact that central processing of vestibular signals is impaired in PD (Colnat-Coulbois et al., 2005; Colnat-Coulbois et al., 2011). While PD is associated with a decrease in automaticity of movement (thus a greater need for conscious control of movement; (Hardeman, Kal, Young, van der Kamp, & Ellmers, 2020; Masters et al., 2007; Nutt et al., 2011; Wu et al., 2015)) it is unlikely that tendencies towards increased CCM are involved in the observed differences, since the subsequent study revealed no effect of increased CCM on visual reliance. While these findings are small and therefore perhaps difficult to interpret, one may argue that they open the door to more informed and nuanced research on the topic.

Wider Perspectives

Key Theoretical Models and Implications

As described in Chapter 1, Peterka's human balance control model (2018) describes how sensory inputs from various senses are integrated and weighted to analyse body movement and produce corrective motion. This model gives some context to our main finding in Study 1, where we see an increase in response to a visual perturbation in one condition compared to another. Peterka's model would suggest that the visual input elicited by the visual perturbation is weighted more heavily in one condition, producing an orientation estimate biased towards the visual information. Thus, a larger sensory error is elicited when this estimate is compared with the "internal reference" and thereby producing increased corrective torque, i.e. a larger postural response. Further elaborations on Peterka's model help to explain why this effect occurs in the Threat condition of the current paradigm; Bronstein (2019) elaborated upon the initial 'internal orientation estimate' stage of Peterka's model, and described a "general comparator" in his model of visual control of posture. In this model, a "comparator" in the CNS assesses the nature of an incoming visual stimulus and uses Bayesian estimation to determine how reliable the visual information is, and therefore whether to increase or decrease visual gain. In this model, any incoming visual information that appears incongruent with other sensory inputs (for example, a visual perturbation that is incongruent with inertial signals) would be weighed up against these other inputs and its reliability interpreted. This model emphasises the persistent nature of visual processing that often seems to supersede other senses relevant to balance, evidenced both by the simple demonstration that, at least on the first presentation, visual signals elicited by a visual perturbation override inertial cues and produce a postural response, and also by evidence of persistent upweighting of vision in several contexts, especially those of increased anxiety (Bronstein et al., 1990; Cousins et al., 2017; Jacob et al., 1995). Importantly, Bronstein (2019) argues that psychological inputs (such as anxiety or rumination) serve to bias the "general comparator" in favour of visual cues, thus increasing the gain of visual input.

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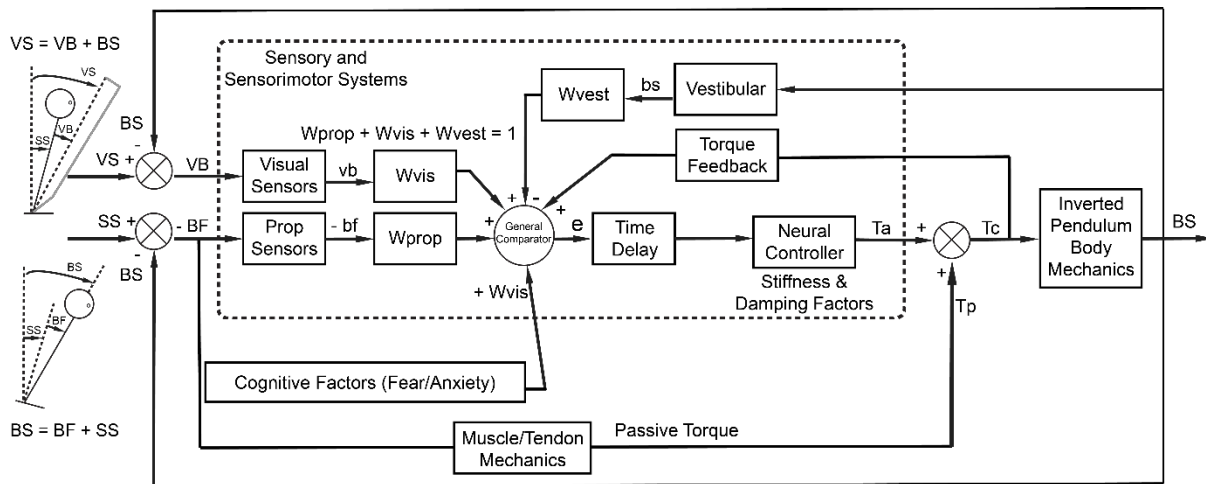


Figure 14. Illustration of the human balance control model required for balance maintenance, adapted from Peterka (2018) and Bronstein (2019). Ta: ankle torque. Tp: passive torque. Tc: corrective torque. BS: body sway. VS: visual surround tilt. VB: VS relative to body sway angle. SS: support surface tilt. BF: BS angle relative to feet angle on support surface. $W_{prop}/W_{vis}/W_{vest}$: weighted proprioceptive, visual, and vestibular sensory contributions.

Together, these models can explain our current findings that anxiety leads to increased visual reliance, whereby anxiety related to posture in the Threat condition biases the comparator towards the visual input generated by the visual perturbation, thereby producing a larger postural response to the perturbation, compared to the non-anxiogenic Ground environment (see Figure 14).

Overall, it is evident that anxiety, especially anxiety related to postural control, affects the way multiple incoming senses are integrated and processed in the brain, with general evidence pointing to an upweighting of visual input (Alharbi, 2017; Cousins et al., 2017; Hainaut, Caillet, Lestienne, & Bolmont, 2011; Jacob et al., 1995; Ohno et al., 2004), and the results from Study 1 showing increased visual weighting with increased anxiety. To return to the issue originally described in Chapter 1, what are the implications of these models and the current results for FOF in OAs? In OAs with FOF, Bronstein's model (2019) would suggest that the anxiety about falling may be biasing their CNS even more towards visual input than the already biased baseline levels due to age. This may in turn lead to increased fall risk through inaccurate interpretations of optic flow leading to inappropriate postural responses, inadvertently pushing the centre of balance beyond the threshold of stability. Using a paradigm similar to the current one (albeit with methods to mitigate any potential ceiling effects) with OAs with and without FOF may reveal more indication of how much anxiety about falling contributes towards the already increased visual reliance.

While the previously discussed models serve to elucidate the observed behaviour of younger adults, and to some extent in older adults, it struggles to fully account for the behaviour we observed in both healthy OAs and OAs with PD+FOG. Anxiety may be playing a part in upweighting

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of vision, but it is not the whole picture. While Bronstein (2019) describes how psychological inputs such as anxiety may bias the nervous system towards visual information, other age- or disease-related mechanisms must also be feeding into this loop to exacerbate this bias. One possibility could be that non-visual inputs, or the initial processing of these inputs, degrade at a greater rate than visual inputs, resulting in increased reliance on the relatively more reliable input. While some have found that the proprioceptive system does not deteriorate as quickly with age as the vestibular and visual systems (Horak et al., 1989; Pasma et al., 2014), little is known about the rates of vestibular processing decline compared to the rate of decline of visual processing. It is possible that vestibular processing mechanisms could become impaired more quickly than vision, which may contribute to the increased reliance on vision we see with age. Alternatively, vision could be upweighted with age compared to vestibular simply because visual aids are relatively more available, and many age-related visual problems are more likely to have been corrected than those pertaining to vestibular function. However, these visual aids (such as glasses to correct presbyopia) are designed to correct low-level visual deficits, which are not thought to have significant effect on self-motion perception for balance (Halperin et al., 2020). Whether or not the relative ease of vision correction compared to vestibular correction is likely to bias the Bayesian system of the CNS towards vision for balance control is perhaps an interesting question for future research.

Regarding the effects of neurodegeneration, while group differences in our study were limited, wider research would suggest increased reliance on visual input, seemingly because other inputs (such as vestibular information and/or proprioception) are unreliable or unavailable. This is evident both in healthy ageing populations (Bugnariu & Fung, 2006; Choy et al., 2003; Franz, Francis, Allen, O'Connor, & Thelen, 2015; Skinner, Barrack, & Cook, 1984), as well as in patients with PD (especially those with FOG; (Huh et al., 2016)), Persistent Postural-Perceptual Dizziness⁷ (PPPD; (Lee, J. et al., 2018; Söhsten, Bittar, & Staab, 2016)), Vestibular Neuritis (Cousins et al., 2014b), and other related vestibular disorders (Staab et al., 2017). In PD+FOG populations particularly, these patients often show an inability to recruit vestibular information for postural control, as described above, reportedly due to impaired processing of vestibular signals (Colnat-Coulbois et al., 2005; Colnat-Coulbois et al., 2011), resulting in evidence of increased reliance on visual information (Huh et al., 2016). While an increase in CCM is observed in many of in these populations (Boisgontier et al., 2013; Chow et al., 2018; Kaski, 2020; Masters et al., 2007; Tjernström, Fransson, Holmberg, Karlberg, & Magnusson, 2009; Wu et al., 2015; Wuehr et al., 2017), the findings from Chapter 5 indicate that increased CCM does not contribute to increased reliance on vision, therefore factors other than

⁷ It should be noted that in PPPD, vestibular function *is* reliable, but the original vestibular disturbance experienced by people with this disorder appears to have biased the CNS against vestibular input.

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anxiety and CCM warrant further investigation to elucidate the mechanisms underpinning these observed biases towards visual information. As discussed in Chapter 3, the impaired ability to reweight could be due to attentional switch problems, therefore the “comparator” (as described in Bronstein’s model (Bronstein, 2019)) could remain ‘stuck’ on vision since it is already biased towards this sensory input. As reviewed in Chapter 4, increased visual reliance in people with PD+FOG is to be expected due to proprioceptive deficits along with age-related decrease in vestibular function which, given the sensory reweighting mechanisms described above, presumably increase the weighting of visual inputs. However, we did not see this clearly in our results, and correlational analyses on the PD+FOG group seemed to indicate that changes in postural response were not due to anxiety. Clearly, further work is necessary to better tease apart the mechanisms involved in sensory reweighting in ageing and clinical contexts.

Research Applications

How might the present findings inform clinical research help those at risk of falling? As we age and become more prone to falling (especially if we become anxious or fearful about falling (Hadjistavropoulos et al., 2011)), how might better balance control strategies be emphasised or learned, and how might anxiety/fear be managed? If anxiety is indeed a factor that contributes increased visual reliance (and therefore potentially decreased stability), interventions designed to simply reduce state anxiety may go some way towards decreasing fall risk in vulnerable groups. Payette and colleagues (2017) found significant associations between Generalised Anxiety Disorder and FOF. Therefore, one useful avenue of research is exploring whether anxiety disorder interventions such as cognitive-behavioural therapy (CBT) have a beneficial effect on fall risk and related fear in those with GAD and FOF, when combined with motor therapy. Indeed, some studies have explored similar interventions directly targeting FOF. Parry and colleagues (2016) employed a CBT approach (a commonly successful intervention for anxiety reduction (Hofmann & Smits, 2008)) alongside usual care for FOF, and found significant improvements in both FOF and depression scores compared with usual care alone. A pilot study conducted by Wetherell and colleagues (2018) documented the effectiveness of an approach combining elements of CBT with exercise and exposure therapy on reducing FOF. However, intervention effects eroded after six months, highlighting the need for further research on how these strategies can be improved upon to maintain long-term effectiveness in reducing FOF.

The current studies have focussed on orthostatic balance control. This is informative when considering orthostatic balance, but it is useful to explore how these findings apply to dynamic tasks – especially when considering that most falls occur during movement such as walking (Talbot,

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Musiol, Witham, & Metter, 2005). We may expect that dynamic sensory reweighting will be more volatile during dynamic gait tasks, with changing environmental features detected both visually and under-foot, as people adapt to their surroundings. Therefore, it is important that these findings may eventually be evaluated in dynamic gait research. Interestingly, Osaba, Martelli, Prado, Agrewal, and Lalwani (2020) unexpectedly observed that OAs' gait was no more altered by visual perturbations than that of YAs during a treadmill task, despite all previous research indicating increase in visual reliance in OAs. They concluded that this was likely because OAs adapt their gait to a much slower speed than YAs, allowing more time for reweighting thus less interference from unreliable visual information, while YAs move much faster, thus are affected by the visual conflict. Evidently, the learned coping mechanisms that OAs develop to counteract the neural changes in sensory reweighting and allow for easier movement must be considered when expanding this research to non-static tasks.

Clinical Applications

The current study used Virtual Reality (VR) to explore visual weighting and postural control, and successfully induced anxiety in participants when they were placed in the environment designed to induce postural threat. As VR technology develops and becomes more versatile (e.g. more portable, with more convincing environments), it may prove to be a very useful clinical tool to reduce postural anxiety in those with FOF, potentially through exposure therapy and practicing safer postural strategies through virtual scenes simulating challenging environments. The innate ability of VR to greatly vary these environments may also lead to greater generalisation of learning. In other words, it could be possible to habituate OAs to anxiety to mitigate any effects of anxiety on sensory processing. Preliminary results from case studies suggest that exposure therapy can be successful in reducing fear of falling and related avoidance behaviour (Robinson & Wetherell, 2018). There is evidence that VR is useful for reducing height-related fear when paired with music (Seinfeld et al., 2015), and research tools such as Toronto Rehabilitation Institute's Challenging Environment Assessment Laboratory (CEAL), which pairs immersive VR with treadmill walking (Campos et al., 2018), have great potential to provide innovative research on therapeutic methods for populations at risk of falling. One study employed a visual perturbation strategy similar to the one used in the current studies in research designed to examine the success of VR training in improving balance control learning, and found positive results, with OAs demonstrating reduced falls after VR training (Parijat, Lockhart, & Liu, 2015). Regarding techniques for non-healthy ageing populations, Kim, Darakjian, and Finley (2017) found no adverse effects when exposing a group of PD patients to a virtual city scene in which they had to walk for 20 minutes, and promoted the use of such head-mounted VR display techniques for therapeutic use. As discussed in Chapter 5, it is possible that

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visual feedback may produce more reliable results in VR experiments, by virtue of increasing the visual awareness of own-body movement. Therefore, providing a virtual body that reflects real-time movements may be a useful consideration for VR-based interventions. One important factor to consider when designing these VR-based interventions, however, is the nature of the virtual environments. Very recent research has found that postural instability (measured via COP sway area) significantly increases between a real-world environment and a virtual environment even with both at ground level (Chander et al., 2020). Previous research has demonstrated that VR-induced postural instability may be minimised when the virtual environment is a duplicate of the surrounding real-world environment (Cleworth et al., 2012), therefore future virtual interventions may benefit from this consideration. Augmented Reality (AR) allows for introduction of virtual objects and scenes into the real-world environment, which may be a useful way forward to address any potential issues with VR-induced instability due to the mis-match between reality and 'virtuality', and has already seen some positive results in early balance training studies with OAs (Mostajeran, Steinicke, Ariza Nunez, Gatsios, & Fotiadis, 2020).

When it comes to the question of how clinical research might develop better interventions for those with impaired motor/sensory systems, the answers are not straightforward. For example, those with PD are potentially relying more on vision because other options are potentially defective – this strategy is perhaps the lesser of two evils (the other being placing more reliance on a misleading proprioceptive/vestibular system). If proprioception and/or vestibular information is unreliable due to impaired processing and/or bias in the feedback due to pathology or arousal, then they realistically do not have any choice other than to rely more on visual input – even if this is likely to be destabilising. While our study on the effects of CCM did not find any effect of directing focus internally on visual weighting, many studies do find that external focus of attention is beneficial for balance control, and propose encouraging external focus in those who are at increased risk of falls. However, due to deficits in proprioceptive feedback, should attempts be made to encourage more external focus in a PD population? Some findings suggest that this would help; external cues do seem to be beneficial for locomotion in people with PD, for example by producing more stable gait (Landers, Wulf, Wallmann, & Guadagnoli, 2005; Rocha et al., 2014; Rochester et al., 2007; Wulf, Landers, Lewthwaite, & Toöllner, 2009) and particularly for those with FOG (Gilat et al., 2018; Ginis et al., 2017; Rahman, Griffin, Quinn, & Jahanshahi, 2008). However, inducing external focus and/or cognitive task difficulty is not necessarily a one-size-fits-all method for improving balance control; some research suggests that an increase in external focus is ineffective or even detrimental to balance control, depending on the abilities of the target group and/or the nature of the focus task (Ellmers et al., 2020; Hardeman et al., 2020; Huxhold, Li, Schmiedek, & Lindenberger, 2006; Kal et al.,

2019). Therefore, interventions using direction of attention and/or distraction techniques for balance improvement evidently need to consider the specific motor and cognitive needs of the individual.

Limitations, Future Directions, Conclusion

Limitations

Both methodological and analytical limitations exist in the experimental sections of this thesis. Perhaps the most obvious of these is the limited-trial paradigm used throughout. This will not be discussed in extensive detail here, since the advantages and disadvantages have been described in previous chapters. Briefly, the decision to only use a single trial per experimental condition has, as one might expect, resulted in large between-subject variability and a potential error in representing visual reliance in a given individual. In some cases, these are difficult to interpret, and could obscure some meaningful results; using a single trial inevitably results in variability in the point in the sway position at which the perturbation was presented, which was not controlled within or between participants. However, since presenting repeated incongruent visual perturbations runs the risk of participants habituating to the stimulation and therefore obscuring any effects of unexpected perturbation (Bronstein, 1986; Bronstein, 2019; Nishiike et al., 2013; Oude Nijhuis et al., 2009), it was decided that a limited trial paradigm would yield the more reliable findings. In the third experimental chapter, the use of 4 trials may indeed have resulted in reweighting that may have obscured effects of internal focus/threat. Since a clear effect of threat was found in the first study, it is very possible that a Type 2 error occurred in Chapter 5 due to the repeated perturbations causing a downweighting of vision. It is clearly difficult to strike the balance between avoiding the confound of habituation versus obtaining sufficient data to be indicative of a particular participants' cognitive state/behaviour. One potential solution to this may be to spread multiple perturbations over several sessions, taking care to maintain variables such as foot position.

Secondly, the selection of outcome measures is potentially problematic. All measures of anxiety and conscious control of movement were self-reported. While using self-report methods are currently the only available avenue to measure CCM, many studies make use of physiological measures to supplement self-reported anxiety data. Galvanic Skin Response (GSR), for instance, is commonly used to quantify physiological arousal. However, GSR does not provide a reliable absolute measure of arousal for any given instant. Furthermore, self-reported anxiety levels tend to correspond well with physiological measures (Cleworth et al., 2019; Kantor, Endler, Heslegrave, & Kocovski, 2001), and previous research using very similar paradigms to the extant studies have also relied solely on self-reported measures for quantifying psychological variables such as anxiety

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(Cleworth et al., 2016). Indeed, LeDoux (2014) argues that physiological response to threat is independent from the conscious psychological experience of anxiety or fear. Contemporary models of fear and anxiety categorise anxiety as a largely cognitive process that, while related to and, to a large extent, driven by physiological response, this conscious experience of processing anxious thoughts is best evaluated by self-reports of that conscious experience, rather than through physiological measures of arousal. Therefore, in the context of this group of studies, self-reported measures of anxiety are more relevant than physiological responses.

More generally, relying on COP as the sole descriptor of postural response has its limitations, especially since participant height and weight were not measured, which influence ground force reactions. Similarly, these studies cannot adequately address the question of how increased stiffening during the Threat condition may have affected the centre of movement (COM) of the body, which was not measured directly. Following previous research, we adopted the perspective of the “inverted pendulum” model, where the body pivots around the ankle (Carpenter, Mark G., Frank, & Silcher, 1999; Johansson, R., Magnusson, & Akesson, 1988), when selecting and interpreting outcomes, but it is possible that this is not the most appropriate model for this specific paradigm. The current studies represent an initial investigation into the effects of postural threat/vection – an initial indication of behaviour with increased age and anxiety. There are many physiological and psychological factors that interact to ultimately generate behavioural responses in the current context. This complexity is compounded by factors such as ageing and associated physiological, neurological and psychological changes. future studies could address these factors by employing a paradigm similar to that of the current study to examine how, for example, the experience of vection affects COM as well as COP for different age groups in the context of increased threat.

Previous research has observed a discrepancy between the experience of vection and actual postural behaviour in response to a visual disturbance (for review see (Saftari & Kwon, 2018)). Vection can be defined as the erroneous sensation of movement that occurs when all or part of the visual field is in motion, and is measured through self-report (Johansson, G., 1977; Saftari & Kwon, 2018). The amplitudes of vection and postural sway elicited from optic flow are positively correlated (Thurrell & Bronstein, 2002), and dependence on vision can predict the strength of experienced vection (Palmisano, Apthorp, Seno, & Stapley, 2014). With age, however, postural sway increases while vection declines; Haibach, Slobounov, and Newell (2009) recorded both postural sway and self-reported ratings of vection from YAs and OAs in response to a moving room in VR. The OAs demonstrated larger postural sway, but lower rates of vection, suggesting that an age-related reduction in proprioceptive feedback may be contributing to increased postural sway. Self-reported sensation of vection was not recorded in any of the studies in this thesis. It is arguable that this

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somewhat limits our interpretations of between-subject responses, since it is possible that the illusion of motion used in the first study, for example, did not induce the sensation of vection to the same extent in OAs than YAs. However, the manipulation of environment to increase anxiety is arguably still valid, and within-group comparisons still indicate a somewhat lesser effect of postural threat on postural response in OAs compared to YAs despite comparable self-reported anxiety levels.

A similar limitation is the failure to assess sensory function in the cohorts that were recruited for this thesis; sensory function differences may have influenced the degree to which a person relies on vision to begin with, thereby potentially affecting between-subject comparisons. However, any major sensory function differences were controlled for through the sample exclusion criteria. For Chapter 4, between-group differences in sensory function were assumed given the nature of PD+FOG, but it must be acknowledged that taking direct sensory function measurements may have improved the between-group analysis of these data. Again, this limitation does not affect within-subject comparisons beyond the potential for carrying out mediation analyses. One factor that may have affected between-condition comparisons is the intrinsic nature of the Threat condition, where a difference in the environment (i.e., the large drop in front of the participants and slight difference in small features on the horizon that were included to provide visual cues about the length of the gully) may have affected optic flow compared to the Ground environment. The use of the fixation point was included to mitigate this effect, as participants were looking at a clear feature that was in the same position in both conditions and controlled for the point at which the participants foveated, thereby better controlling for optic flow. Furthermore, all distinct objects in the environment were positioned beyond the fixation point, which was itself beyond the normal near point of convergence (about 6-10cm). Since the vast majority of each scene is beyond the convergence point, we do not expect that this would have been a significant confound of any observed effects of Threat. The velocity of the perturbation was identical between conditions, so the actual flow rate across the retina was the same; however, the perception of that flow may have differed due to differences in contrast, which may have been richer in the Threat condition given the large depth of ground surface in front of the participant compared to the flat surface in the Ground condition. Nonetheless, while contrast can affect optic flow perception (Stone & Thompson, 1992), the areas with greatest contrast have consistency between conditions. However, we must accept that the intrinsic difference in the visible environment between conditions may have had some effect on optic flow, and future studies should account for this when using similar paradigms. Creative solutions that manipulate anxiety specific to fear of falling while keeping the visual scene unaltered may mitigate this issue. Young and colleagues (2015) used a “trapdoor” paradigm to elicit

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FOF-specific anxiety where participants were made to believe that some areas of the raised surface they walked on would collapse if stepped on, when in fact the entire walkway was solid. This method allows an increase in fall-related anxiety without needing to change any of the visual scene. Future studies using VR could employ this method virtually, thereby preserving consistent optic flow between baseline and threat conditions while presenting a visual perturbation.

Finally, it is important to discuss the potential limitations associated with the choice of perturbation size. Following the pilot study using three different perturbation amplitudes/velocities, the smallest perturbation was chosen for subsequent empirical studies due to the risk of a potential ceiling effect occurring with the use of larger perturbations, and because it minimised the risk of impact on the response to the subsequent trial i.e., it was subtle enough to be integrated within the balance task so that the risk of habituation to the perturbation was lessened. However, we must acknowledge that using a larger perturbation may have produced different responses to those we have observed throughout this thesis, therefore we cannot generalise the observed results to contexts with greater sensory disparities. Nevertheless, the smaller perturbation is arguably more similar to the subtle sensory disparities experienced in the real world (such as a momentary slight sway when experiencingvection), where it is uncommon to experience rotations of the speed of the largest perturbation. Therefore, the small perturbation was judged to be the most sensitive manipulation for measuring the subtle responses to small changes in visual weighting in the sensory reweighting system. While other studies using visual perturbations (e.g., (Keshner et al., 2004)) observed greater COP responses than those observed in the current studies, these experiments used larger perturbations that were arguably less representative of natural postural sway. The aim of the current study was to measure postural sway in response to a stimulus that was more reminiscent of natural sway, therefore we used an arguably more representative stimulus at the cost of smaller and more volatile responses. Again, we argue that this results in response observations that may be more ecologically valid.

Directions for Future Research

While inclusion of electromyographical (EMG) or centre of mass (COM) measures were not able to be included in the current studies, this paradigm would certainly benefit from including EMG and COM measurement to support the kinetic (i.e. COP-related) measures. Measuring muscle activity using EMG would potentially clarify what underlying muscular mechanisms are at work during postural threat in the current paradigm, and whether they would align with the current kinetic findings. Moreover, given the differences between kinematic and kinetic outcome measures observed in previous studies using postural threat and/or presentation of incongruent sensory cues

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(Bugnariu & Fung, 2006; Cleworth et al., 2016), it is possible that the mechanisms underlying COM-specific postural behaviour in different contexts such as increased threat, internal focus, age, or neurodegenerative disease may differ to what we see in the kinetic data.

As mentioned in the limitations, a different perturbation size may produce different results. Future studies could endeavour to test whether varying perturbation sizes and speeds produce different effects on VEPRs, whilst mitigating potential habituation effects.

Concluding Remarks

This thesis aimed to address the broad question of how anxiety affects sensory integration for balance control, particularly with regards to reliance on visual input. The present results answered this question through the progression of studies conducted for the thesis – the main novel findings being that postural threat and the corresponding heightened feelings of anxiety do increase reliance on visual information, and that, to a variable degree, healthy ageing and neurodegenerative disease also produce an upweighting of visual input. The mechanisms behind the latter are unlikely to involve anxiety or increased conscious movement control, given the current findings, but these warrant further research using more comprehensive additional measures.

The thesis also generated new questions, such as which mechanisms other than anxiety and conscious control of movement are also responsible for changes in visual weighting and balance control (particularly in healthy adults and those with neurodegenerative disease), and how the wider findings so far may be used to inform more effective and individualised therapeutic techniques for those at high risk of falls and injury. Whether increased visual reliance with anxiety is due to the dominant nature of visual input compared to inertial input, increased attention to threat-relevant stimuli, and/or other factors is a question that may be answered by carefully designed future paradigms. It is hoped that future research will endeavour to answer these remaining questions through robustly designed experiments, informed by the knowledge that this thesis has generated.

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APPENDIX

Ethics Approval – Pilot Study



College of Health and Life Sciences Research Ethics Committee (DLS)
 Brunel University London
 Kingston Lane
 Uxbridge
 UB8 3PH
 United Kingdom
 www.brunel.ac.uk

16 May 2017

LETTER OF APPROVAL

Applicant: Anna Fielding
Project Title: Effects of FoF on Balance Control
Reference: 5531-LR-May2017- 7193-2

Dear Anna Fielding

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- ◆ A18 – PIS – In the section 'Why have I been invited to participate?' you were asked in the previous feedback to add your inclusion criteria re age and number of participants you are seeking. You have only added the age criteria. Please add the number of participants you are seeking.
- ◆ A18 - Advert - It would be preferable to have contact with yourself via your Brunel email only rather than publish your personal mobile telephone number.
- ◆ The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- ◆ Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- ◆ The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee.
- ◆ Approval to proceed with the study is granted subject to receipt by the Committee of satisfactory responses to any conditions that may appear above, in addition to any subsequent changes to the protocol.
- ◆ The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study.
- ◆ You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair

College of Health and Life Sciences Research Ethics Committee (DLS)
 Brunel University London

EFFECTS OF POSTURAL THREAT ON VISUAL REWEIGHTING

Ethics Approval – Study 1



College of Health and Life Sciences Research Ethics Committee (DLS)
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30 April 2018

LETTER OF APPROVAL

Applicant: Anna Fielding
 Project Title: Effects of FoF on Balance Control
 Reference: 5531-A-Apr2018- 12608-2

Dear Anna Fielding

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- ♦ The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- ♦ Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- ♦ The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee.
- ♦ The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study.
- ♦ You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair

College of Health and Life Sciences Research Ethics Committee (DLS)
 Brunel University London

EFFECTS OF POSTURAL THREAT ON VISUAL REWEIGHTING

Ethics Approval – Study 2



College of Health and Life Sciences Research Ethics Committee (DCS)
 Brunel University London
 Kingston Lane
 Uxbridge
 UB8 3PH
 United Kingdom
 www.brunel.ac.uk

18 October 2017

LETTER OF APPROVAL

Applicant: Miss Amy Masilvec

Project Title: ANALOGY LEARNING IN PARKINSONS

Reference: 7299-MHR-Oct/2017- 8503-4

Dear Miss Amy Masilvec

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- ♦ The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- ♦ Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- ♦ The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee.
- ♦ Approval to proceed with the study is granted subject to receipt by the Committee of satisfactory responses to any conditions that may appear above, in addition to any subsequent changes to the protocol.
- ♦ The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study. You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair

College of Health and Life Sciences Research Ethics Committee (DCS)
 Brunel University London

EFFECTS OF POSTURAL THREAT ON VISUAL REWEIGHTING

Ethics Approval – Study 3



College of Health and Life Sciences Research Ethics Committee (DLS)
 Brunel University London
 Kingston Lane
 Uxbridge
 UB8 3PH
 United Kingdom
www.brunel.ac.uk

10 October 2019

LETTER OF APPROVAL

APPROVAL HAS BEEN GRANTED FOR THIS STUDY TO BE CARRIED OUT BETWEEN until 30.09.2020

Applicant (s): Ms Anna Fielding

Project Title: Various Effects of Anxiety in Virtual Reality Environments

Reference: 12617-A-Oct/2019- 20591-1

Dear Ms Anna Fielding

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- You will need to amend this end date on all corresponding forms - any adverts, PIS and Consent form.
- As your study is for a period greater than twelve months, you are required to submit at the end of the first (and subsequent) year(s) a report to the College Research Ethics Committee to confirm that your study is still progressing, if any changes have been made or are required and if there have been any issues with the study. Please submit this to DLS-Ethics@brunel.ac.uk by 31/10/2019.
- The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee.
- The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study.
- You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair of the College of Health and Life Sciences Research Ethics Committee (DLS)

Brunel University London