Reliance on the visual frame of reference in ageing across different sensorimotor tasks : from perception to walking

Catherine Perséphone Agathos

NNT : 2016SACLS351

THESE DE DOCTORAT
DE
L'UNIVERSITE PARIS-SACLAY
PREPAREE A
L'UNIVERSITE PARIS-SUD

ECOLE DOCTORALE N° 566

Sciences du Sport, de la Motricité et du Mouvement Humain

Spécialité de doctorat : Sciences du Sport et du Mouvement Humain

Par

Mme Catherine Perséphone Agathos

Reliance on the visual frame of reference in aging across different sensorimotor tasks: from perception to walking

Soutenu à Orsay, le 7 octobre 2016

Composition du Jury :

M., Papaxanthis, C.	Professeur, Université de Bourgogne - INSERM	Président
Mme, Luyat, M.	Professeur, Université Lille 3	Rapporteur
M., Bourdin, C.	Professeur, Aix-Marseille Université - CNRS	Rapporteuse
M., Do, M.C.	Professeur, Université Paris-Sud	Examinateur
Mme, Decker, L.	Maître de Conférences, Université de Caen Basse-Normandie - INSERM	Examinatrice
M., Isableu, B.	Maître de Conférences, Université Paris-Sud	Directeur de thèse
Mme, Assaiante, C.	Directrice de Recherches, Aix-Marseille Université - CNRS	Co-directrice de thèse
Mme, Bernardin, D.	Professeur Associé, Chaire Industrielle Essilor/CRSNG, Université de Montréal	Tutrice Industrielle

«Beautiful, ethereal

this dizziness, – be careful, you'll fall. Don't look at me,

for my place is this wavering – this splendid vertigo.»

The Old Woman in Black to the Young Man

Yannis Ritsos, *Moonlight Sonata*, 1956

For my Families, whom I cherish.

Acknowledgements

I would like to thank Prof. Marion Luyat and Prof. Christophe Bourdin for having accepted to evaluate this manuscript. Thank you also to Prof. Charalambos Papaxanthis, Prof. Manh-Cuong Do and Dr. Leslie Decker for agreeing to be part of the jury of this thesis. Thank you all for your genuine interest, it was a great pleasure discussing my work with you.

I am immensely grateful to my three supervisors Brice Isableu, Christine Assaiante and Delphine Bernardin. I consider myself very lucky to have had the opportunity to work with such rigorous and passionate researchers; the eloquence alone with which you would discuss our work has been inspiring. You have each brought forth your own unique approach and the fusion of your expertise has been a rewarding experience. Thank you for introducing me to whole new worlds of research that I am now intent on pursuing further. There is a certain naive disappointment in not being able to explore all the questions that arise from a research project, but I am grateful to all three of you for fuelling my curiosity in wanting to do so – but also for helping me set the limits in practice. Thank you for sharing your ambition, for being demanding and for asking the right questions instead of showing me the answers. Never have I learned as much as during this PhD, from theory to methodology, to writing and presenting. Thank you also for setting an exciting and positive tone in every interaction of ours, you truly break the stereotype of the cold and distant PhD supervisors! Brice, thank you first of all for thinking of me in the conception of this project and inviting me on this journey. Christine, thank you for every time you hosted me in your friendly lab. I stand to thank you both for your approachability and commitment despite the distance, for your guidance and for running alongside me in the final sprint. Delphine, I could have never asked for a better manager. Thank you for knowing when to push me and when to support me, for letting me understand you would be by my side whenever I should need you. Our meetings constructing and deconstructing hypotheses together remain major highlights of these past years. Thank you for your incredible patience, for helping me organise my thoughts and come out of our discussions each time ever more motivated and genuinely appreciative of the beauty of our project.

I thank all of the Vision Sciences department and colleagues in Bastille (and beyond) for providing such a warm work environment, for their encouragement and for our interesting collaborations. I am grateful to Bernard Bourdoncle for accepting me into his team at Essilor. Thank you for giving us the green light to implement our experimental ideas and giving me the opportunity to attend multiple workshops and conferences. I owe special thanks to Anne-Catherine Scherlen and Konogan Baranton whose contributions truly added value to this work. Anne-Catherine, thank you for taking me under your wing as well in the beginning of my PhD; for introducing me to Low Vision, for providing special insights into our work and for your continuous support and enthusiasm. Konogan, thank you for saving me from the abyss of my data sheets! Thank you for your genuine interest, your calm and positive temperament and your guidance in helping me develop clean(er) and logical methodological tools. It’s been a pleasure working with you. Jean-Luc, you’ve been a great office buddy, thank you for providing the right balance between work and

diversion. Thank you also for your help and counsel in the set-up of the experiments and analysis. Coralie, thank you for your support and your company during all those late night work sessions.

A huge thank you to all who participated in the experiments (preliminary and final), thank you for your availability, your patience and your beautiful data!

Whether aware of their influence or not, I am immeasurably grateful to all those that have stood by me during this PhD, within and beyond the work-place. I will start by apologising to those I may miss, as listing everyone who has contributed to my well-being over the past three and a half years would require a chapter in its own.

Special thanks go to my friends in Paris who made this city my home. Marion, Adèle, your friendship marked the beginning of this and made work so much more comfortable and fun. Thank you for your help throughout, for every break, for every encouragement to keep working and every opportunity to stop and go out. Thank you especially for being there beyond the walls of Essilor, for your enthusiasm and original plans – even if we didn't always get to fulfil them. Colas, my friend in the field, on your own you've been the post-grad office I never had access to: sharing work and play. Thank you for listening when my ideas were not well developed, for your assistance and counsel, for your encouragement and giving me perspective; and of course for all the conversations that started in the courtyard and ended in the bar.

I am indebted to my wonderful neighbours, Antoine and Sammy. Thank you for all the hours you spent on my work and teaching me new tools, for your patience and humour in front of my constant indecisiveness. But thank you more for being part of the family, for looking after me and for pushing me back to machine mode when I lost confidence. Maria, Julia, thank you for sharing your lives and not just your space, for helping to build a warm (and truly enviable) home and a new family. Clara (and Quentin in passage), thank you for taking over and adding your touch. Thank you for your cheerfulness and for enduring, with Maria, the final stages of my write-up – and for letting me monopolise the apartment. Maria, I will say it: thank you! For every wake up call, every coffee, every song, for every distraction and every push back to work. Thank you for picking up when it mattered, for your comfort and your fun (and funny, rest assured) and optimistic attitude. Julia, thank you for your enthusiastic support, for the proactive spirit you shared – and for not disappearing after moving out. Yvon, it was a pleasure co-working with you, thank you for taking care of me and the flat, for keeping the mood up. Stéphanie, thank you for your concern, reassurance and heartfelt encouragement. Matthieu, thank you for the study sessions, the concerts and the moral and technical support.

Near or far, I am grateful to Kallina, Melissa, Evi, Aloi, Gianni and Stella. Thank you for your support and for believing in me. Eri, thank you for being there despite the distance, sharing the pain and cheering me on. Matt, thank you for your comfort during what was arguably the most difficult part of this journey. Pamela, thank you for your encouragement and understanding; for trusting me with Elaïa and adding a beautiful new

dimension to my life during this PhD. Thank you to everyone from the London and Brussels crews for all the stories and for keeping my spirits high with your (real or virtual) company.

Finally, I would never have gotten to this point without the continuous and unconditional backing of my family and words will not do their significance justice. I am grateful to my parents, Helene and Spiro, for setting the bar high and believing we may actually surpass it. Thank you for your time, your affection and the treasures you've provided us with all these years. Kelly, Niko, it's "siblings by chance, friends by choice", thank you for holding me up, pushing me on. I am grateful for your love.

Contents

I. *Chapter 1: Theoretical Framework*

I.1 General Introduction

Healthy aging entails degradation in multiple levels of sensorimotor control and behaviour, stemming from peripheral sensory to central processing deficits. Although not exacerbated to the point of pathology, such age-related deficits are considered to affect daily living tasks in old adults, ultimately leading to loss of independence and health risks, most notably falls. In a recent review, Ambrose et al. (2013) have identified fall risk factors in physiological as well as pathological aging. These notably include a cautious and stiff gait pattern, diminished muscle strength, poor depth perception and stereo-acuity as well as reduced attention capacities (especially divided attention) and executive functions. The present research was conducted with these considerations in mind given the rapid aging of our population (World Health Organisation, 2015). Posture and gait in the elderly have received a lot of attention, with the important interaction between cognition and movement gaining ground in recent years as well (Rosano, Rosso, & Studenski, 2014). Significant gaps remain however in the characterisation of the increased reliance on the visual frame of reference (visual field dependence) that accompanies aging, and, crucially, in terms of how this affects sensorimotor control. In young adults, visual field dependence is associated with specific cognitive, adaptive and sensorimotor behaviour. For example, more visual field dependent individuals use more rigid inter-segmental coordination strategies for stabilisation (Isableu et al., 2003) and are slower to adapt to novel situations of sensory discordance (Brady et al., 2012; Isableu et al., 2010). Taken together with age effects, the reported increase in visual field dependence in old age may pose risks in daily living activities and is indeed considered a risk factor for falls as well (Lord & Webster, 1990).

In this thesis, we shall attempt to bridge the gaps existing in the literature between visual field dependence, postural control (from stance to walking) and aging; and to examine the implications of reliance on the visual frame of reference with age and at different levels of sensorimotor complexity. An originality of this thesis is to consider this question during the adult life span involving a comparison between young, middle-aged and old adults, in order to highlight a possible transition period. The main research questions may be summed up as follows:

1) Are there age-related changes in cognitive and sensorimotor functions associated with greater reliance on the visual reference frame?
2) How does the age-related increased visual field dependence influence postural and walking behaviour?

   and
3) Are there indices that translate such a reliance on the visual reference frame during postural and walking tasks?

Such insights are bound to extend current knowledge on the effects of aging on the interplay of perception and action, provide elements to consider in order to maintain autonomy and to provide more personalised care and may contribute to finer design of training and rehabilitation protocols for frailer old adults. Moreover, by exploring these questions from young to middle-aged to old adulthood, we may develop sharper insights into the evolution of visual field dependence and the associated mechanisms for perceptivo-motor control.

I.2 Reliance on the visual frame of reference : spatial referencing and beyond

I.2.1 Frames of reference for spatial orientation and individual differences

Spatial orientation is the assessment of one's own and/or other objects' position, orientation, and movement. It entails information processing for both cognitive and sensorimotor operations. To interact with one's environment the body's position, orientation and motion are perceived with respect to different frames of reference (FoR), like coordinate systems, based on representations of the gravitational vertical and/or invariants (axes and planes) relative to this: visual direction (e.g. walls vs. ground surface), gravito-inertial force (GIF) direction and the body support surface. In this thesis, we shall group together the last two FoRs using the term *egocentric* frame of reference given that the body-based vestibular and somatosensory modalities are the bases of exploiting the GIF and support surface as opposed to the visual FoR. By referring to the visual FoR, one's subjective perception of verticality is based on the visual cues perceived. On the other hand, by referring to the egocentric FoR, one's subjective vertical is based on his/her *internal* representation of the vertical, based on somatosensory or vestibular cues (Anastasopoulos, Bronstein, Haslwanter, Fetter, & Dichgans, 1999; Barbieri et al., 2008; Barra et al., 2010; Borel, Lopez, Péruch, & Lacour, 2008; Lopez, Lacour, El Ahmadi, Magnan, & Borel, 2007; Manckoundia, Mourey, Pfitzenmeyer, Van Hoecke, & Pérennou, 2007; Mittelstaedt, 1983; Perennou, Amblard, Leblond, & Pelissier, 1998).

When walking through an uncluttered environment, a hallway for example, sensory cues from different modalities may convey the same information about one's motion and the setting. The optic flow and gravito-inertial acceleration generated by the body's motion are sensed by the visual and vestibular systems respectively. The inclination of the ground support surface and the body's orientation with respect to it are conveyed by somatosensory cues such as cutaneous information from the podal contact with the ground, joint position sense of the different body segments, graviceptors as well as visual cues (e.g. depth, perspective) which provide a relationship of the body and other visual references (e.g. vertical walls). In such a situation, that is, when environmental and/or task constraints are minimal, different frames of reference can

be used for spatial orientation in an equally efficient manner. Under more complicated or dangerous tasks/settings, reliance on one frame of reference may prove more appropriate. For example, referring to the visual frame of reference will not be of much use to someone trying to maintain upright balance in a rapidly accelerating train. In other words, frame of reference redundancies in low posturally-demanding tasks suggest that there exist various optimal and equi-efficient modes of spatial referencing (i.e., vicarious processes (Reuchlin, 1978)). The lesser redundancy between FoRs in more demanding tasks causes a reduction in the potentially optimal numbers of modes of spatial referencing in order to accomplish the task.

Robust individual differences have been demonstrated among humans showing a stable preference in frame of reference selection over time. Behaviour associated with the reliance on the visual frame of reference in particular has received a lot of focus. Witkin and colleagues (Witkin, Dyk, Faterson, Goodenough, & Karp, 1962; Witkin et al., 1954a) originally developed the concept of perceptual-cognitive 'styles' based on individuals' susceptibility to a distracting or misleading visual context. Individuals showing reliance on the visual FoR in perceptual visual disembedding tasks were thus termed visual field dependent (FD), while individuals unaffected by the visual context were termed visual field independent (FI). These authors proposed that an individuals' style falls within a continuum from greater visual field dependence to independence, rather than being of binary nature. Robust tests evaluating visual field dependence are subjective vertical estimation tasks when faced with a disorienting visual context. The most notable and frequently used is the rod and frame test (RFT) (Witkin & Asch, 1948) whereby one must adjust a tilted rod enclosed in a tilted frame to the orientation of the gravitational vertical. The dynamic analogue of the RFT is the rod and disc test (RDT) (Guerraz, Poquin, & Ohlmann, 1998), where a kinetic visual disturbance, a rotating patterned disc, is provided instead of the static tilted frame. The embedded figures test (EFT) (Witkin, Oltman, Raskin, & Karp, 1971) is another widely used assessment of visual field dependence requiring participants to find and manually trace simple figures embedded in more complex forms. While this test does not tap into spatial orientation, correlations exist with the subjective vertical tasks suggesting that visual field dependence describes both perceptual and cognitive aspects of interacting with one's environment. Indeed, research examining the manifestation of visual field dependence beyond spatial orientation has been abundant in the field of experimental psychology linking the subjective vertical tests to the EFT.

I.2.2 Manifestations of reliance on the visual frame of reference

Research has revealed that individual differences extend to postural control in the preferential use of the visual (Isableu, Ohlmann, Crémieux, & Amblard, 1997; Brady et al., 2012; Isableu, Ohlmann, Crémieux, & Amblard, 1998; Streepey, Kenyon, & Keshner, 2007) or egocentric (Isableu & Vuillerme, 2006; Brady, Peters, & Bloomberg, 2009; Kluzik, Horak, & Peterka, 2005) FoR during stance and walking. Postural

control requires the integration of visual, vestibular and somatosensory information. According to the FoR selected, different sensory cues are weighted and integrated in order to maximise the reliability of the information associated with a certain modality and, consequently, its contribution to postural control for stance and locomotion.

Individuals showing greater reliance on the visual FoR also exhibit differences in postural control compared to their visual field independent counterparts. It should be noted, however, that the paradigms used to best reveal such differences involve not only providing incongruent visual with respect to egocentric cues but also doing this under conditions threatening postural stability, for example via manipulations of the base of support, such as narrowing it (Streepey et al., 2007) or generating mechanical perturbations (Keshner, Kenyon, & Langston, 2004; Mergner, Schweigart, Maurer, & Blümle, 2005). The differences that emerge between FD and FI individuals appear both in how visual cues are preferentially exploited and on postural behaviour. Studies have revealed that FD individuals orient their bodies with respect to the visual FoR to a greater extent than FI individuals when faced with a large tilted frame while standing (Isableu et al., 1997; Isableu et al., 1998) or when viewing an oscillating scene while walking on a treadmill (Brady et al., 2012). In addition, FD adults rely more heavily on dynamic visual cues for postural balance (Isableu et al., 2010; Isableu et al., 1998). Individuals relying on the visual FoR show greater postural instability (Isableu et al., 1997; Isableu et al., 2010; Isableu et al., 1998; Streepey et al., 2007) and a more rigid, bottom-up segmental stabilisation strategy at the head as well as the trunk level (Isableu et al., 2010; Isableu et al., 2003) when placed in challenging postural situations and provided with incongruent visual cues. In particular, FD individuals tended to stabilise their head on the underlying trunk segment while the more FI individuals stabilised their head in space. Moreover, increasing the difficulty associated with maintaining postural balance was found to accentuate differences between FD and FI individuals, with the more visual field dependent participants showing greater probability of fall as well (Isableu et al., 2010; Streepey et al., 2007).

Finally, beyond the sensorimotor behaviours described above, research has revealed that visual field dependence affects higher order processes such as attention and perceptual reaction time (Yan, 2010), and adaptation and sensory reweighting (Brady et al., 2012; Gueguen, Vuillerme, & Isableu, 2012; Isableu et al., 2010). These studies suggest that even among young healthy individuals, being reliant on the visual FoR can reduce the ability to identify the most appropriate sensory cues to exploit and inhibit or at least delay the shifting of weight attributed to egocentric signals. These are important associations to bear in mind when examining the implications of visual field dependence in old age, given the existence of age-related deficits as well.

I.2.3 Suggested factors leading to increased reliance on the visual frame of reference

Given that increasing the difficulty of postural tasks enhances the dynamics of balance, which would be perceived mainly via vestibular and somatosensory modalities, a greater reliance on the visual FoR under challenging postural conditions would imply that egocentric signals are either ignored or more difficult to process for FD individuals. Studies examining visual field dependence in postural control suggest therefore that the greater weight placed on visual inputs is associated with a downweighting of vestibular and somatosensory inputs, possibly due to a reduced ability to exploit or a neglect of such egocentric cues (Bernardin, Isableu, Fourcade, & Bardy, 2005; Isableu et al., 2010; Isableu et al., 2003; Streepey et al., 2007). Moreover brain imaging studies provide evidence of reciprocal inhibition in the reweighting mechanism of visual-vestibular integration for self-motion perception (Brandt, Bartenstein, Janek, & Dieterich, 1998; Deutschländer et al., 2002), while cortical areas responding primarily to vestibular stimulation have been found to respond to somatosensory stimulation as well (Bottini et al., 2001). These interactions reveal the dominance of the visual over an egocentric modality and vice versa in order to avoid ambiguity between percepts. The principal of reliance on the visual FoR being associated with a downweighting of egocentric cues may be further supported by considering populations identified as predominantly visual field dependent such as children (Assaiante & Amblard, 1992; Bagust, Docherty, Haynes, Telford, & Isableu, 2013; Forssberg & Nashner, 1982), old adults (we shall focus on this population in detail further along) and individuals with certain pathologies such as Parkinson's disease (Azulay et al., 1999; Bronstein, Hood, Gresty, & Panagi, 1990; Azulay, Mesure, Amblard, & Pouget, 2002), labyrinthine defective and visual vertigo patients (Bronstein, Yardley, Moore, & Cleeves, 1996; Guerraz et al., 2001), people suffering from neglect (Funk, Finke, Müller, Utz, & Kerkhoff, 2011) and in some cases stroke (Bonan et al., 2004; Marigold & Eng, 2006; Slaboda, Barton, Maitin, & Keshner, 2009; Slaboda & Keshner, 2012) and deafferented patients (Blouin et al., 1993; Bringoux, Scotto Di Cesare, Borel, Macaluso, & Sarlegna, 2016). Research on these populations has provided precious insights on the possible underlying neural and peripheral sensory bases of visual field dependence.

Visual field dependence follows a trend decreasing from childhood to adulthood and increasing again in old age. Upon the acquisition of independent stance and walking, greater weight is attributed to visual information under conditions of sensory conflict and/or in challenging postural situations (Assaiante & Amblard, 1993; Forssberg & Nashner, 1982). As evidenced in healthy young visual field dependent adults, the greater reliance on the visual FoR in young children also is associated with problems in adaptation and dynamic sensory reweighting (Forssberg & Nashner, 1982). These authors have highlighted an underdevelopment of postural adaptation mechanisms, though it is not clear whether this would be due to peripheral sensory immaturity or central, higher order immaturity. While the influence of visual, especially peripheral, cues to postural control increases with age up until around 6 years (Assaiante & Amblard, 1992), a change occurs at around the age of 6-7 years whereby visual cues are no longer predominantly upweighted

(Assaiante & Amblard, 1993). This period of developmental transition in fact coincides with the acquisition of a new sensorimotor skill: the head stabilisation in space (as opposed to *en bloc*, on the trunk) strategy. This strategy is considered to be of vestibular origin (Bronstein, 1988; Pozzo, Berthoz, Lefort, & Vitte, 1991), facilitating the integration of sensory signals by stabilising the head and ultimately preserving lateral balance.

Studies on the above patient groups further corroborate the sensory integration and weighting issue associated with visual field dependence. On the one hand the visual field dependence observed in labyrinthine and deafferented patients revealed the consequence of deficits in the periphery on sensory reweighting; on the other hand, examining the central deficits of the aforementioned patient groups has provided insights as to the brain areas that are associated with an increased reliance on the visual FoR and involved the multisensory integration and reweighting processes for perceptivo-motor operations such as postural control. The latter has been cleverly tackled by examining visual field dependent patients with patients of similar conditions (e.g. brain damage with and without neglect, cerebellar versus Parkinsonian patients). The common finding is that, depending on the condition, there exist difficulties in processing vestibular and/or somatosensory cues but also, and perhaps more importantly, in the ability to appropriately (re)weigh sensory cues from different sensory modalities. The regions of the brain associated with greater reliance on the visual FoR if impaired lie generally in the parietal-insular area (Miyai, Mauricio, & Reding, 1997), while it has been shown that stroke patients with lesions in the right hemisphere show greater reliance on the visual FoR than do patients with left hemisphere lesions (Bonan et al., 2004). More specific cortical and sub-cortical areas associated with visual field dependence when impaired are the superior temporal gyrus, temporo-parietal junction, insula, frontal operculum, putamen, thalamus and the basal ganglia, that is, areas involved in multisensory integration and reweighting for postural adaptation and visuo-spatial estimation (Bronstein et al., 1990; Funk et al., 2011; Miyai et al., 1997).

Finally, we should mention the influence of sensorimotor – and type of sensorimotor – expertise on frame of reference reliance. Populations of healthy individuals have been characterised as relying on the visual or the egocentric FoR depending on their experience in either open- (e.g. tennis, football) or closed- (e.g. track and field, swimming) skill dominated sports categories respectively (Liu, 2003; McLeod, 1985). The extent of sensorimotor experience however also impacts one's ability for postural adaptation and exploitation of the egocentric FoR. For example, expert gymnasts are able to compensate for the lack of visual information by exploiting egocentric cues compared to non-gymnasts (Vuillerme, Teasdale, & Nougier, 2001); on the other hand, less active individuals show greater reliance on the visual FoR, probably due to their lack of reinforcement of egocentric cue exploitation through physical activity.

I.3 Reliance on the visual frame of reference and aging

I.3.1 Perceptivo-motor behaviour associated with increased reliance on the visual frame of reference in healthy old adults

Over the past decades a great many studies have revealed an increase in reliance on the visual FoR with old age. This greater reliance compared to younger adults has been demonstrated with the classic tests in line with the conceptualisation of visual field dependence by Witkin and his colleagues, i.e. via the RFT, RDT and EFT (e.g. (Eikema, Hatzitaki, Tzovaras, & Papaxanthis, 2012; Kobayashi et al., 2002; Marendaz, 1984; Markus, 1971; Panek, Barrett, Sterns, & Alexander, 1978; Schwatz & Karp, 1967; Slaboda, Lauer, & Keshner, 2011)) as well as by revealing a greater influence or contribution of visual cues on postural control and adaptation in stance and walking (e.g. (Berard, Fung, & Lamontagne, 2011; Borger, Whitney, Redfern, & Furman, 1999; Bugnariu & Fung, 2007; Eikema et al., 2012; Franz, Francis, Allen, O'Connor, & Thelen, 2015; Jeka, 2010; Jamet, Deviterne, Gauchard, Vancon, & Perrin, 2004; Poulain & Giraudet, 2008; Slaboda et al., 2011; Straube, Botzel, Hawken, Paulus, & Brandt, 1988; Yeh, Cluff, & Balasubramaniam, 2014)). Indeed there is evidence of a greater reliance on visual feedback for postural control in old age (Bugnariu & Fung, 2007; Franz et al., 2015; Jeka, 2010; Sundermier, Woollacott, Jensen, & Moore, 1996; Yeh et al., 2014), that this is accompanied by greater instability (Borger et al., 1999; Franz et al., 2015; O'Connor, Loughlin, Redfern, & Sparto, 2008; Simoneau et al., 1999; Sparto, Furman, & Redfern, 2006; Wade, Lindquist, Taylor, & Treat-Jacobson, 1995) especially when both the visual and somatosensory modalities are perturbed, (Borger et al., 1999; Eikema et al., 2012; Eikema et al., 2013; Franz et al., 2015; Hay, Bard, Fleury, & Teasdale, 1996; O'Connor et al., 2008; Slaboda et al., 2011; Sparto et al., 2006; Teasdale, Stelmach, Breunig, & Meeuwsen, 1991; Teasdale, Stelmach, & Breunig, 1991) revealing in this way also a slower or reduced sensory reweighting and postural adaptation capacities. The last studies in fact point to an inability and/or slowness on the one hand to assess which sensory cues are more reliable in order to upweight them, and on the other, to exploit the egocentric frame of reference. The perceptivo-motor behaviour associated with greater visual field dependence in old age is suggested to be linked to age-related deficits in the vestibular and somatosensory systems (Judge, King, Whipple, & Clive, 1995; Manchester, Woollacott, Zederbauer-Hylton, & Marin, 1989) as well as linked to central deficits (Berard et al., 2012; Eikema et al., 2013) which affect how information is processed, how sensory cues are (re)weighted and integrated, but also, how motor tasks are executed.

I.3.2 Age-related peripheral sensory and central deficits associated with spatial orientation and perceptivo-motor control

Vestibular and somatosensory degeneration are considered more severe and/or to occur earlier in life compared to visual degradation (Jamet et al., 2004; Lord, Clark, & Webster, 1991a). At the vestibular level, cell loss and structural changes have been documented as early as middle-age (Sloane, Baloh, & Honrubia, 1989). Focus should remain however on the implications of age-related changes on the functional level of vestibular function. Indeed, old adults show deficits in the gain and phase of the vestibulo-ocular reflex (VOR) (Paige, 1994). Moreover, in certain activities of daily living suppression of this reflex is required, for example, during sit-to-stand, stand-to-walk transitions and walking on stairs, where the gaze should follow head orientation. The suppression of the VOR in such tasks has been shown to be compromised in old adults identified as having a greater risk of fall (Di Fabio, 2001). It is indeed fallers that show greatest deficits in vestibular function among – at least seemingly – healthy old adults (Liston et al., 2013). It is common for fallers to report sensations of dizziness and unsteadiness, though vestibular function is rarely assessed in falls clinics. Moreover, Liston and colleagues revealed that in fact these individuals present greater peripheral vestibular impairment. The somatosensory system undergoes changes with age as well. These involve deficits in multiple structures leading to a reduction in proprioceptive acuity, increased tactile thresholds and ultimately affect balance (Shaffer & Harrison, 2007).

Normal aging also entails deficits in central cognitive and executive functions in addition to multisensory integration. There is evidence pointing to defects in central integrative mechanisms with age rendering the sensory reweighting process ever more challenging and slow (Stelmach, Teasdale, Di Fabio, & Phillips, 1989; Teasdale & Simoneau, 2001; Berard et al., 2012; Eikema et al., 2012). The reduction of available cognitive resources and overall slowness of information processing (Salthouse 2000) and of interhemispheric transfer (Jeeves & Moes, 1996) with age makes the reweighting of the available sensory information for sensorimotor control a cognitively demanding task (Redfern, Jennings, Martin, & Furman, 2001) that is subject to prioritization and competition effects (Eikema et al., 2012). In addition, inhibitory capacities also decline with age (Chao & Knight, 1997; Dustman, Emmerson, & Shearer, 1996) leaving older adults with greater difficulty in resisting distraction, for example in disregarding erroneous visual cues during locomotion (Berard et al., 2012). Functional MRI studies have revealed that old adults show greater recruitment of multisensory areas (Heuninckx, Wenderoth, & Swinnen, 2008) and in general recruit more brain regions, possibly to compensate lower level deficits (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005).

Finally, changes in brain structures with age alter how the body is controlled. Significant age effects have been found in the primary motor and somatosensory cortices (Salat et al., 2004) and these authors also showed global cortical thinning from middle age. Studies have shown an age-related degeneration of the

cerebellum (Raz, Gunning-Dixon, Head, Williamson, & Acker, 2001; Raz et al., 2005) which is important for movement timing and coordination (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). The prefrontal (Good et al., 2001; Jernigan et al., 2001; Raz et al., 1997; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003) and parietal (Good et al., 2001; Resnick et al., 2003) cortices also show grey matter atrophy, while motor control is more dependent on both these regions in old adults.

I.4 Rationale

I.4.1 Research Questions

Given the above theoretical framework, certain important gaps emerge regarding how aging affects one's interaction with their environment at both the perceptual and sensorimotor level. While aging entails central and peripheral deficits, these are not to the point of pathology in order to make direct comparisons to the visual field dependent patient populations presented above. Moreover, questions remain on age-related deficits that could be associated to the increased reliance of old adults on the visual FoR in the context of performing and maintaining autonomy in activities of daily living. On the other hand, while we may have evidence of the postural behaviour related to visual field dependence this cannot be directly extrapolated to old adults' postural control in stance and walking in daily life, such as when faced with visual (e.g. luminosity of environment) or motor (sit-to-stand, stand-to-walk) transitions, maintaining postural balance in perturbing visual environments (e.g. in crowds, sidewalks of busy roads) and while driving. Indeed studies have revealed that sedentary old adults are more visual field dependent than their more active age- and education- matched counterparts (Karp, 1967; Markus & Nielsen, 1973; Rotella & Bunker, 1978) while a sedentary lifestyle poses greater mortality risk. More visual field dependent elders also show difficulties in performing dual-tasks (Maylor & Wing, 1996), have more driving accidents (Guerrier, Manivannan, & Nair, 1999; McKnight & McKnight, 1999) and have been identified as fallers (Barr et al., 2016; Lord & Webster, 1990). There is therefore a need to better understand and characterise visual field dependence in old age.

Visual, vestibular and somatosensory cues are weighted (and dynamically reweighted) and integrated in order to maximise the reliability of the respective modality following maximum likelihood estimation (Ernst & Banks, 2002; Oie, Kiemel, & Jeka, 2002). Considering the CNS as a Bayesian estimator (Ernst & Bülthoff, 2004), we may regard preferred modes of spatial referencing as priors in individuals' interactions with their environment. Developing or applying models of sensory integration in the context of visual field dependence is beyond the scope of this thesis. Rather, by manipulating the reliability of visual and

somatosensory information, we may infer the respective sensory contributions and the effect of FoR reliance as a prior on our tasks. We thus consider reliance on the visual frame of reference as a prior whose strength increases with age. Consequently however, as the power of the prior increases, actual afferent signals are downweighted or attention is biased toward specific sensory cues.

In this context many questions may arise with respect to sensorimotor control in old age. How does the prior influence old adults' perception of their environment and their behaviour therein? Can this be qualified during postural and locomotor tasks? Old age is associated with a multitude of changes, are there specific age effects that relate to exacerbated visual field dependence? Are signals associated with the egocentric frame of reference weaker, are they ignored or is visual input simply upweighted? And, importantly, how do visual field dependence and its effects on perceptivo-motor behaviour change throughout adulthood? In this section, we will elaborate on the aims and protocol designs of the subsequent experimental chapters in order to provide some answers to the above questions. These will allow us to ultimately debate on the major question of this thesis: *does visual field dependence in old age reflect a mode of adaptation or rigid compensation?*

I.4.2 Tools and Methodology

Cross-sectional design

The common practice in aging research on the influence of vision on posture and walking is to evaluate old adults against young. This however leaves open the question of when transition occurs in the observed behaviour. Middle-aged adults are underrepresented in perceptivo-motor research as a study group on their own, often omitted or included in the younger or older participant classes. There is evidence however of an increase in visual field dependence in middle-age (Lee & Pollack, 1978; Panek et al., 1978; Poulain, Giraudet, & Dobrescu, 2004) along with sensory decline as well. Both the proprioceptive (Goble, 2010; Hurley, Rees, & Newham, 1998) and vestibular system (Sloane et al., 1989) show degradation, while middle-age is the onset of presbyopia. It is therefore important to also examine how changes in these modalities, studied mostly in isolation, affect tasks where multimodal integration is required and how this may evolve into old age. Does middle-age represent a transition period in perceptivo-motor behaviour or does the transition appear from middle-age to old adulthood? We therefore recruited adults from three age groups to participate in our studies: younger than 45 years old, 45 to 65 years old and over 70 years old.

The visual frame of reference in our experiments

In order to examine visual field dependence, a perturbing visual stimulus is provided and one's tendency to exploit or ignore this visual reference reveals their relative reliance on it. Although we discuss visual field dependence and its increase in a general manner with age, we shall more specifically examine three aspects of reliance on the visual reference frame: a cognitive, visuo-spatial reliance, reliance for spatial orientation and reliance for self-motion perception. As we will see in the experimental chapters that follow, the three are linked and we may indeed speak of reliance on the visual reference frame and its evolution with age and influence on perceptivo-motor tasks using a single term. There is a slight nuance however between reference reliance for spatial orientation and for self-motion perception as is discussed in Chapter 3. Moreover, in chapters 3 and 4 we did not deem it relevant to examine the cognitive aspect of visual field dependence in the context of postural and locomotor behaviour. This was chosen, rather, to tap into the cognitive component of visual processing in our endeavour to better characterise visual field dependence with age and its association with other age-related changes as is done in Chapter 2.

The group embedded figures test (GEFT) was used to qualify visual field dependence as a cognitive, visuo-spatial reliance. The visual reference frame in this task is the complex, misleading form hiding the simple figure therein. For spatial orientation, the subjective visual vertical was evaluated in two tasks: the rod and frame test (RFT) and the rod and disc test (RDT). Here, the visual reference frame is a tilted frame and a rotating disc respectively which may 'attract' one's subjective vertical (indicated by the adjustment of a tilted rod within the visual context) in the orientation of the tilt or rotation. Finally, for self-motion perception during postural and locomotor tasks, the visual reference frame provided is ground optic flow, i.e. a visual stimulus providing speed and direction information on one's motion. How reliance on this visual frame of reference is qualified is a question of this thesis in itself and will be detailed below.

The egocentric frame of reference

In this thesis, we consider the egocentric frame reference as based on vestibular and somatosensory information, though emphasis is given on the latter. Exploiting the egocentric frame of reference would mean accurately sensing and processing one's orientation and motion with respect to the environment using body-based cues, i.e. motion and orientation sensors of the vestibular and somatosensory systems and podal pressure and touch sensors, as well as internal models of orientation and motion. For spatial orientation specifically, reliance on the egocentric frame of reference was assessed by examining the contribution of such cues on the construction of one's subjective vertical. Egocentric information about the orientation of one's body influences the orientation of their subjective vertical. A tilted rod, presented without a conflicting

visual context, was adjusted by our participants while standing upright and tilted laterally at 70°. In each case, the body's axis would 'attract' one's subjective vertical if the egocentric reference frame is exploited, though the effect while tilted is considered to be mainly of somatosensory origin.

Building a visual sensorimotor profile of our participants

We evaluated several functions related to visual perception in order to examine possible associations with visual field dependence and its increase with age. Visual acuity, contrast sensitivity, stereo-acuity and visual field extent are known to degrade with age (Haas, Flammer, & Schneider, 1986; Lord, Clark, & Webster, 1991b; Owsley, 2011). While visual function has been dismissed as contributing to visual field dependence (Barrett, Cabe, & Thornton, 1968), we deemed it necessary to confirm our observations would not be influenced by possible age effects on these variables in our participants. Moreover, they have been identified as fall risk factors in some studies (de Boer et al., 2004; Freeman, Munoz, Rubin, & West, 2007; Klein, Moss, Klein, Lee, & Cruickshanks, 2003; Lord et al., 1991b). Parallel (central vs. peripheral) visual attention processing is also known to decline with age (Ball, Owsley, & Beard, 1990; Edwards et al., 2006; Matas, Nettelbeck, & Burns, 2014; Sekuler, Bennett, & Mamelak, 2000) and is associated with detriments in both visual sensation and cognition (Wood & Owsley, 2013). We therefore included the useful field of view test (UFOV) in our protocol, in particular for its second and third components which evaluate parallel and selective attention processing ability respectively. Finally, visual fixation stability was also examined as a basic measure of oculomotor control in order to examine its potential contribution to spatial orientation. Visual fixation stability is associated with both a visual and somatosensory percept; therefore if an age-related degradation exists, this would imply noise in both sensory signals and may influence the exploitation of a certain frame of reference.

I.4.3 Answering our research questions

Characterisation of increased visual field dependence with age by examining associations with changes in cognitive and sensorimotor functions and egocentric dependence with age

In our first experimental chapter, we sought to qualify reliance on the visual reference frame with age in the context of age-related changes in visual sensorimotor perception and processing and with respect to reliance

on the egocentric reference frame. We examine whether the greater reliance on the visual frame of reference with age is linked to a reduced reliance on the egocentric frame of reference. That is, does the increased visual field dependence constitute a preferred mode of spatial referencing while either frame of reference may be exploited efficiently or is it associated with a diminished ability to exploit the egocentric frame of reference? Given that visual field dependence is associated with peripheral visual sensitivity and processing ability as well as attention (Goodenough, Oltman, & Cox, 1987; Isableu et al., 1998; Yan, 2010), we sought to examine the relationship of parallel visual attention processing, via the UFOV test with reliance on the visual reference frame. Assessment of visual fixation stability as an oculomotor function on the other hand provides insights on the exploitation of both frames of reference.

Given the decline in visual sensory and central processing ability with age, the greater reliance on the visual frame of reference in old age may appear as a paradox. Visual field dependence is a mode of spatial orientation and need not necessarily be linked to the *quality* of the visual input. This is elaborated in the discussion of Chapter 2. Moreover, if the ability to exploit the egocentric frame of reference is reduced with age, shifting reliance to the visual frame of reference may indicate a compensation strategy, irrespective of the age-related deficits in visual perception and processing. Indeed, it is often suggested that a greater *relative* degradation of the vestibular and somatosensory systems is associated with the observed shift towards greater reliance on the visual frame of reference (Judge et al., 1995; Manchester et al., 1989).

Characterising visual field dependence in terms of self-motion perception in the context of aging

In Chapter 3, we examined how the influence of approaching and receding linear ground optic flow on posture may be dependent on aging. We created conditions of sensory discordance by providing a visual self-motion stimulus of forward/backward translation while participants were required to maintain their (anteroposterior) position in space. Two postural tasks were introduced giving rise to different levels of sensory integration complexity: quiet standing (QS) and stepping in place (SIP). During QS, the visual motion information provided conflicted with vestibular and somatosensory cues which indicate a quasi-static body condition. During SIP on the other hand, the sensory conflict was less pronounced given that vertical and lateral movements of the head are relevant to the perceived visual motion since such movements occur when walking forwards or backwards, while the podal contact with the ground surface became intermittent. We were interested in whether ground optic flow perception would influence head and body orientation and translation (in the case of SIP) during these tasks, whether the effect would be enhanced when the podal contact with the ground surface was no longer constant due to stepping in place and whether old adults would be more responsive than the younger participants. We hypothesised that old adults' greater reliance on the visual frame of reference for spatial orientation would show greater sensitivity to optic flow.

Identifying signatures of visual field dependence while walking in the context of aging

In the fourth and final experimental chapter, we considered how ground optic flow influenced the control of walking. Kinematic modulations of gait occur when confronted with simulated optic flow (Baumberger, Flückiger, & Roland, 2000; Mohler, Thompson, Creem-Regehr, Pick Jr, & Warren Jr, 2007; Pailhous, Ferrandez, Flückiger, & Baumberger, 1990; Prokop, Schubert, & Berger, 1997; Varraine, Bonnard, & Pailhous, 2002) given that such stimuli are visually scaled to the biomechanical and motor features of locomotion. Moreover no differences have been identified between young and old adults on the guiding effect of optic flow on gait (Chou et al., 2009; Schubert et al., 2005; Konczak, 1994). We therefore focused on the possible differential influence of optic flow on the head-trunk stabilisation strategy between our three age groups and on whether specific behaviour was associated to a greater reliance on the visual frame of reference. As we saw above, a rigid *en bloc* head stabilisation strategy has been observed in visual field dependent population such as children walking on beams (Assaiante & Amblard, 1993) and Parkinson's disease patients (Mesure, Azulay, Pouget, & Amblard, 1999) while walking and in healthy young visual field dependent adults under visual perturbation during postural tasks (Isableu, Ohlmann, Crémieux, & Amblard, 2003). We therefore considered whether greater reliance on the visual frame of reference in old adults would be evidenced by a more rigid head stabilisation strategy compared to younger adults and under conditions of optic flow compared to natural walking conditions.

Adaptation or compensation?

The aim of this thesis is to better characterise visual field dependence in old age. Examining the results of our experimental protocols combined may allow us to better understand both the possible underlying causes of increased reliance on the visual FoR with age but also its operation on the daily life of older adults by extrapolating the observed behaviour from perception to posture to walking. The sensorimotor factors, postural and walking behaviour associated with increased visual field dependence in old age combined can help us determine whether such reliance on the visual FoR is:

a) an adaptation to optimise perceptivo-motor behaviour in view of age-related deficits, that is, maximise weight and salience of reliable information while minimising those of less reliable cues; or
b) a compensation *due* to age-related deficits, which means, however, that visual information is not exploited in a useful manner but by default.

One focus of our discussion therefore shall lie on how our observations argue in favour of the first or second assumption of visual field dependence in old age.

I.4.4 Hypotheses

Our first hypothesis lies on the evolution of visual field dependence across adulthood. While reliance on the visual FoR may be considered a preferred mode of spatial referencing in young adults, we suppose that with the age-related changes that occur onwards, the relative central and peripheral degradations that appear will affect how the visual FoR is actually exploited. Additionally, we should observe behaviour associated with visual field dependence in middle-aged as well as, albeit to a greater extent, in old adults, particularly in the tasks posing greater threat to the maintenance of postural stability, namely during stepping in place and upon the initiation of gait, but also under the more ecologic, approaching flow. Our second hypothesis lies on the relative association of reliance on the visual and egocentric FoR with age. We propose that visual field dependence is not merely a preferred mode of spatial referencing over egocentric dependence but rather that it is associated with a reduced ability to exploit the egocentric FoR (Bernardin et al., 2005; Gueguen et al., 2012; Isableu et al., 2010; Isableu, Fourre, Vuillerme, Giraudet, & Amorim, 2011). As such, we expect that a) old adults will be less able to assess their own position/orientation/motion based on egocentric cues and that b) this is inversely related to their ability to do so using visual information and to postural and locomotor behaviour associated with visual field dependence. Third, we hypothesise that the reliance on the visual FoR for perception (tilted frame, rotating disc) and posture/walking tasks (optic flow) should be correlated. We also expect to observe greater differences in behaviour with respect to visual field dependence during stepping in place and upon the initiation of gait. Finally, we actually suppose two types of visual field dependence among old adults: functional (relying heavily on visual FoR but appropriately exploiting visual cues, adaptable as young visual field dependent adults) and over-sensitive (relying heavily on the visual FoR to compensate for age-related deficits, inflexible). The difference between these types of reliance on the visual FoR would be due to the severity of age-related deficits, the former remaining a *preferred* mode of spatial referencing while the other constitutes a *default* mode. Furthermore, degradation with respect to egocentric perception may be a factor leading to visual field dependence, the exacerbated age-related deficits in all sensory modalities, however, as well as in central processes may lead to relying on the visual FoR as a default spatial referencing mode. This would be the case regardless of the appropriateness of using the visual FoR, regardless of the accuracy of the resulting perception of one's self and their environment's spatiotemporal attributes and regardless of the resulting postural and locomotor behaviour in terms of the information that may be gathered from the motor actions but also the risk in maintaining balance.

II. *Chapter 2: Sensorimotor and cognitive factors associated with the age-related increase of visual field dependence*

In this first experimental chapter, we considered factors that may be associated with the greater reliance on the visual FoR observed with age. We chose to examine first of all how reliance on the egocentric FoR evolves throughout adulthood in order to better understand if preferential referencing with respect to visual cues in old age may be linked to a reduced ability to exploit egocentric cues or whether the FoRs associated with each type of sensory input remain equi-efficient. Additionally we examined visual fixation stability and parallel attentional visual processing ability (via the useful field of view – UFOV – test). Both these factors were selected as age-effects would alter not only how visual information is perceived but also i) how it is processed while providing a measure of attentional capacity as well in the case of the UFOV, and ii) the associated somatosensory input stemming from eye movements during the fixation task – a basic measure of occulomotricity.

This chapter has been published in AGE and is available at *http://dx.doi.org/10.1007/s11357-015-9805-x*.

Agathos, C. P., Bernardin, D., Huchet, D., Scherlen, A. C., Assaiante, C., & Isableu, B. (2015). Sensorimotor and cognitive factors associated with the age-related increase of visual field dependence: a cross-sectional study. *AGE, 37,* 1-19.

II.1 Introduction

Spatial orientation is the assessment of one's own and/or other objects' position, orientation, and movement, and involves information processing for both cognitive and sensorimotor operations. When interacting with their environment, humans select appropriate frames of reference for spatial orientation depending on the challenge of the setting and/or the task. Our ability to routinely perceive and control our spatial orientation is based on the functional alignment of egocentric reference frame axes (Fourre et al., 2009; Isableu et al., 2009; Isableu et al., 2010) either on directions within a gravito-inertial field or on surrogates of the direction of gravity e.g., axes within the visual frame of reference (walls, ground, ceiling). Depending on the task-specific inertial-acceleration constraints and demands (Isableu et al., 2009), axes of the body's different coordinate systems can be advantageously exploited, each in association with distinct frames of reference (Fourre et al., 2009; Guerraz, Poquin, Luyat, & Ohlmann, 1998; Guerraz et al., 1998; Guerraz, Luyat, Poquin, & Ohlmann, 2000; Pagano & Turvey, 1995). When the body's sensory systems do not register an

acceleration pattern, frames of reference are highly congruent and redundant. This means that different frames of reference could be used for spatial orientation in an equally efficient manner according to the principle of vicariance (or interchangeability) (Reuchlin, 1978), leading thereby to large inter-individual differences.

Robust differences amongst individuals have been demonstrated in frame of reference selection for certain spatial tasks indicating the existence of 'perceptual styles', whereby an individual expresses a stable preference over time to exploit one mode of spatial referencing among others. Witkin and colleagues (Witkin et al., 1962; Witkin et al., 1954a) proposed to rank individuals' perceptual style along a continuum from visual field independence to dependence . They further theorised these perceptual styles as the operation of a differentiation in perceptivo-cognitive functioning (global vs. analytic), extending beyond spatial orientation (Witkin et al., 1954b). A perceiver is considered more or less visual field dependent, i.e. using the visual field as a frame of reference for spatial orientation, based on his/her ability to consider or ignore, respectively, misleading, distracting or conflicting contextual visual information; or, more generally, the ability of a subject to dissociate an element from its context and reuse it in a different one.

Research has revealed that visual field dependence affects attention, perceptual response time, accident involvement (Bailleux, Marendaz, & Ohlmann, 1990; Mihal & Barrett, 1976; Yan, 2010), postural strategies (Isableu et al., 1997; Isableu et al., 1998; Isableu et al., 2003), and adaptation and sensory reweighting (Brady et al., 2012; Gueguen et al., 2012; Isableu et al., 2010; Viel, Vaugoyeau, & Assaiante, 2010). Enhanced probability of fall is also observed in young and healthy subjects under difficult stance conditions when confronted to perturbing visual information (Isableu et al., 2010; Streepey et al., 2007). Furthermore, visual field dependent individuals are more sensitive to peripheral visual information, such as motion and orientation cues (Amblard, Crémieux, Marchand, & Carblanc, 1985; Isableu et al., 1998; Streepey et al., 2007). A shift towards greater visual field dependence has been reported in old adults (Eikema et al., 2012; Kobayashi et al., 2002; Marendaz, 1984; Markus, 1971; Panek et al., 1978; Poulain et al., 2004; Schwatz & Karp, 1967; Slaboda et al., 2011). However, the determinants leading to this age-related shift in frame of reference selection have not been well defined. Visual field dependence is associated with higher risk for old adults in daily living tasks due to its attentional and sensorimotor implications. Motor control in itself is more attentionally demanding with age, requiring additional cognitive resources (Seidler et al., 2010). Studies have shown that greater visual field dependence in old adults is associated with postural equilibrium alterations, increasing risk of fall (Eikema et al., 2012; Jamet et al., 2004; Lord & Webster, 1990) and leads to more difficulty to perform dual tasks (Maylor & Wing, 1996). Moreover, the implication of adaptation and sensory re-weighting difficulties for old adults (Bugnariu & Fung, 2007; Eikema et al., 2012; Eikema et al., 2013; Slaboda et al., 2011; Slaboda & Keshner, 2012) means risk is even greater under sensory perturbation (e.g. walking on uneven terrain) or whilst in unfamiliar environments where vision in necessary to guide action. Identifying and understanding frame of reference selection with age can help predict performance, adaptation capability in new tasks/environments and provide guidelines for the design of new training procedures for old adults in order to preserve/regain autonomy. In the present study, we investigated factors

possibly associated with increased visual field dependence in old age, by considering functions that are both known to degrade with age and important for spatial orientation and sensorimotor control: reliance on the egocentric frame of reference, visual fixation stability and divided and selective attention for processing peripheral visual information (useful field of view, UFOV).

The weighting of visual information for postural (Borger et al., 1999; Bugnariu & Fung, 2007; Jamet et al., 2004; Poulain & Giraudet, 2008; Slaboda et al., 2011; Straube et al., 1988) and locomotor (Berard et al., 2011) tasks has been shown to increase with age, affecting old adults' stability. Several studies have attributed the upweighting of visual input in old adults to greater somatosensory and vestibular age-related deficits (Judge et al., 1995; Manchester et al., 1989). These latter inputs are used to construct and update one's internal models, leading to a dynamic internal representation of the body in space which combines efferent and afferent information and resolves sensory ambiguities (Cullen, Brooks, Jamali, Carriot, & Massot, 2011; McIntyre, Berthoz, & Lacquaniti, 1998; Merfeld, Zupan, & Peterka, 1999). This dynamic, internal representation or body schema (De Vignemont, 2010; Morasso & Sanguineti, 1995; Paillard, 1999) is the basis of the egocentric, as opposed to the visual, frame of reference. It has been shown that internal models modulate the perception of the vertical (Barra et al., 2010), taking into account one's perception of the body's longitudinal (Z) axis, or 'idiotropic vector' (Mittelstaedt, 1983). Body verticality perception has been investigated in young and old adults (Barbieri, Gissot, & Pérennou, 2010; Schwatz & Karp, 1967) to examine the evolution of egocentric spatial orientation with age. These studies demonstrated alterations of the body schema with age, possibly due to somatosensory deficits (Boisgontier & Nougier, 2013; Deshpande & Patla, 2005; Shaffer & Harrison, 2007; Woollacott, 1993). However, the relationship between increased visual field dependence and reduced egocentric referencing has not been investigated directly in old adults.

Oculomotor signals contribute to perceptual knowledge and sensorimotor control for egocentric referencing, as they participate in the kinematic proprioceptive chain linking the eye to the foot (Roll & Roll, 1988). Moreover, experiments on fixation tasks have revealed the role of eye position signals for head location perception (Lewald & Ehrenstein, 2000), while studies using prisms have uncovered the role of oculomotor signals for postural control (Kapoula & Lê, 2006). The tiny eye movements involved in gaze fixation maintain a centrally viewed point in focus, and keep peripheral visual information salient. The ability to maintain stable eye position may thus affect the exploitation of the egocentric frame of reference as well as visual information processing. Simulated fixation instability in healthy adults, by inducing retinal slips, has revealed the importance of oculomotor stability on complex tasks requiring peripheral visual information gathering (Macedo, Crossland, & Rubin, 2008). Furthermore, it has been reported in previous studies that peripheral visual cues are mainly involved in balance control in children as well as adults (Assaiante & Amblard, 1995; Assaiante, Mallau, Viel, Jover, & Schmitz, 2005) and limitations in peripheral perception affect stability in old adults (Manchester et al., 1989). Visual fixation stability is therefore important for both visual information processing and for its somatosensory contribution and inherently impacts equilibrium and spatial orientation of the whole body. Although it is known that oculomotor control is affected by age (Paige, 1994; Pelak, 2010), there is a discrepancy in the literature with regard to aging on visual fixation stability. While some reports indicate greater instability with age (Hotson & Steinke, 1988; Pelak, 2010; Sekuler &

Ball, 1986), other studies have found no (Crossland, Morland, Feely, von dem Hagen, & Rubin, 2008; Kosnik, Kline, Fikre, & Sekuler, 1987; Shallo-Hoffmann, Sendler, & Mühlendyck, 1990) or limited (Herishanu & Sharpe, 1981) age effects.

Considering the importance of peripheral visual information processing for spatial orientation and the oculomotor consequences of reduction in this ability, we deemed pertinent the evaluation of peripheral visual information processing within our study. With old age, degradation of the peripheral visual field has been documented (Jaffe, Alvarado, & Juster, 1986). What is more marked, however, and more detrimental for old adults, is the shrinking of the attentional visual field, or useful field of view (UFOV) (Ball et al., 1990; Edwards et al., 2006; Matas et al., 2014; Sekuler et al., 2000). UFOV reduction with age has implications on daily living tasks, including driving (Ball, Owsley, Sloane, Roenker, & Bruni, 1993; Owsley et al., 1998) as it implies both visual sensory and cognitive decline (Wood & Owsley, 2013). UFOV testing assesses speed of visual processing for detection and localisation of central and peripheral targets under conditions of divided visual attention and in the presence and absence of visual clutter. In addition, age-related UFOV shrinkage has been revealed in manual (Beurskens & Bock, 2012) and locomotor tasks (Reed-Jones, Reed-Jones, & Hollands, 2014). Changes in oculomotor behavior have been observed with UFOV decline in old adults. Scialfa and colleagues (Scialfa, Kline, & Lyman, 1987) have proposed a model whereby old adults take smaller samples of a visual scene and scan these more slowly than young adults. Visual search studies have also revealed that old adults make more (Scialfa, Thomas, & Joffe, 1994) as well as illicit (Beurskens & Bock, 2012) saccades to compensate UFOV shrinkage.

In the present paper, we seek to establish whether the greater reliance on the visual frame of reference with age is linked to a reduced reliance on the egocentric, somatosensory-based, frame of reference (or egocentric dependence). In this context, examining visual fixation stability can help elucidate the contribution of this basic oculomotor function to egocentric spatial orientation with age. In addition, evaluating the UFOV could reveal links between the visual and somatosensory contribution of the eyes for spatial orientation with age, considering that visual attention and peripheral visual information processing ability is already known to correlate with perceptual style (Goodenough et al., 1987; Isableu et al., 1998; Yan, 2010). A visual examination was also included in our study to ensure that our data were not biased due to deficits in or age effects on certain visual functions. Poor visual acuity (Lord et al., 1991a), contrast sensitivity and stereopsis (Lord & Menz, 2000) have been identified as factors affecting postural stability under challenging situations for old adults as well as risk factors for falls, though there is some discrepancy between studies for the latter (Ambrose, Paul, & Hausdorff, 2013).

We chose a cross sectional design involving young, middle-aged and old adults, in order to better understand the increasing reliance on the visual frame of reference with age. In cognitive and behavioral research studies middle-aged adults are often not included or are classified as old adults as often as they are classified as young. Reports have identified an increase in visual field dependence during middle age (Lee & Pollack, 1978; Panek et al., 1978; Poulain et al., 2004). However, factors or mechanisms related to this increase were not investigated or were inconclusive (Lee & Pollack, 1978; Lee & Pollack, 1980). Sensory changes are known to occur in middle age, most notably the onset of presbyopia, affecting perceivers' ability to focus on

near distances. Proprioceptive acuity has also been shown to decrease from young to middle-aged adulthood (Goble, 2010; Hurley et al., 1998) and degradation of the vestibular system also occurs around middle-age (Sloane et al., 1989). Changes in cognitive function are less well defined. Hence, in this study we were interested in observing how frames of reference are used for spatial orientation in middle-age and what factors may contribute to specific reference frame selection.

Our primary hypothesis was twofold. We supposed increased visual field dependence with age to be correlated to reduced egocentric dependence. Furthermore, a diminished reliance on the egocentric frame of reference should be associated with greater visual fixation instability, supporting the idea that greater visual field dependence and reduced egocentric dependence with age may be partly due to enhanced uncertainty within the eye - foot proprioceptive chain, leading to neglect of somatosensory inputs. Our secondary hypothesis considered that UFOV reduction with age leads to increased eye movements to gather spatial referencing information. These movements may contribute to increasing noise in the proprioceptive chain as well, and weakening proprioceptive self referencing would constitute an additional factor leading to upweighting the visual frame of reference. We therefore expected UFOV reduction to correlate with visual fixation instability (noisier oculomotor signal) as well as visual field dependence. Finally, we expected middle-aged adults' behavior to fall between that of young and old adults revealing a progressive evolution in the parameters evaluated.

II.2 Methods

II.2.1 Participants

A total of 58 volunteers participated in the study. They were divided into three age groups: 20 young adults (YA, 10 males, 10 females, age: 31.7 ± 6.4 years), 18 middle-aged adults, (MA, 7 males, 11 females, age: 51.5 ± 5.6 years) and 20 old adults (OA, 10 males, 10 females, age: 74.1 ± 3.7 years). Participants were free of visual, neurological, musculoskeletal, cardiovascular and vestibular impairments. They all had a binocular visual acuity of at least 0.10 logMAR with normal or corrected to normal vision. Participants wearing glasses were fully adapted to their lenses. The experimenters verified that differences in visual acuity between the refractive correction worn and optimal correction were under 0.10 logMAR. Visual equipment was kept during the visual field and egocentric dependence tests, optimal refractive correction was worn for all other examinations for best corrected visual acuity. Cognitive function was checked with the Mini Mental Status Examination (MMSE). Scores below 25 warranted exclusion. Old adults lived in the community and reported having a fairly active lifestyle. All volunteers were informed of the different test procedures and provided written consent to participate. All tests were performed with the approval of the local ethics committee in accordance with the Declaration of Helsinki.

Visual examination, visual fixation instability and UFOV evaluation were grouped into an experimental session of 1 ½ hours. A second experimental session of the same duration was performed to evaluate visual field and egocentric dependence. Experimental sessions were randomized for all participants and spaced apart by one week on average.

II.2.2 Visual Examination

Four standard tests were completed: binocular visual acuity, binocular contrast sensitivity, stereoscopic acuity and monocular visual field. Visual acuity, i.e. fine detail perception, was measured using the ETDRS© chart at 100% contrast. The evaluation was performed binocularly at a viewing distance of 3 m. Binocular contrast sensitivity was assessed using the Pelli-Robson chart (Pelli, Robson, & Wilkins, 1988) at a medium spatial frequency of 3 cycles/°. For MA and OA, the chart was viewed with an addition of 0.75 δ to avoid blurry vision due to the loss of accommodation capacity. The test was performed at a distance of 1 m. Stereoscopic acuity, i.e. 3D perception, was evaluated using the Fly and Wirt Points vectograms of the Titmus Test. Participants viewed the vectograms as they would read a book, at a distance of 40 cm. The participants wore their optimal refractive correction with an addition of 2.5 δ and polarised glasses. The Fly test is a gross assessment of 3D perception, whilst the Wirt Points test measures the stereoscopic threshold. Monocular visual fields were evaluated via kinetic microperimetry (MP1©, Nidek Technologies, Padova, Italy). A target was displayed centrally (a white cross, subtending 2° x 1° and projected at a simulated distance of 5 m) and calibrated to the visual acuity of the participant on the microperimeter. A 10 dB, size III target (0.43°) moved from one of 8 cardinal positions at 20° eccentricity towards the centre at a speed of 1.5°/s. The measurement was made monocularly for each eye, the other one being covered during the evaluation. Participants fixated the central cross and had to respond once they perceived the peripheral stimulus. A map of visual field was thus obtained for each eye in order to check there were no major deficits in the perception of peripheral visual information.

II.2.3 Visual field and egocentric dependence

Visual field dependence was evaluated with the Group Embedded Figures Test (GEFT), the Rod-and-Frame Test (RFT) and the Rod-and-Disc Test (RDT). Egocentric dependence was evaluated with a subjective vertical estimation task under two postural conditions, referred to here as the Rod-and-Body Test (RBT).

To evaluate the cognitive component of visual field dependence, all participants completed a validated French version of the GEFT (Oltman, Raskin, Witkin, & Press, 1971). This assessment of visual field dependence is commonly used in studies of ageing perceptual style and occasionally alongside visual search paradigms. The test was administered individually, under and with strictly identical conditions and instructions. Participants were asked to find and manually trace hidden forms embedded within complex figures. Two parts were scored, each composed of 9 figures and participants had 5 minutes to complete each part. Scores indicate the number of missed or incorrect items out of the 18. Higher scores therefore denote greater reliance on the visual frame of reference. Visual field dependent participants have a global rather than analytic approach in perceiving and thus have greater difficulty in finding the embedded figures. The visual field dependence reported using this test involves more elaborate cognitive processing than in the subjective vertical tests (RFT and RDT). The GEFT paradigm also comes close to the UFOV 2 and 3 subtests of divided and selective visual attention by tapping into the cognitive component of visual processing.

All participants also performed three tests of subjective vertical estimation: the RFT, RDT and RBT. The RFT and RDT reveal the degree of visual field dependence by assessing the effect of a tilted frame and rotating disc, i.e. the contribution of static and dynamic visual cues, respectively, on subjective vertical estimation. The RBT reveals the degree of egocentric dependence by assessing the contribution of body orientation cues in subjective vertical estimation. The participant's task was to rotate a rod towards the vertical. To limit the duration of the experimental session and thus avoid fatigue, the participants were instructed to respond as quickly as possible, but without compromising accuracy. Response time has been shown to be unrelated to performance on the RFT (Bagust, Docherty, & Razzak, 2013). Procedure and instructions described by Oltman (Oltman, 1968) were followed for the RFT and adapted for the RDT and RBT. Three examples of the vertical were given: visual vertical (wall ridges or door frames), gravitational vertical (space rocket or plumb line) and postural vertical (erect body).

A computerised program was developed for each test using Python software and stimuli were projected (768 x 1024 dpi) on a 1 m² screen. The stimuli were a white rod centered within a white tilted square frame (RFT), within a rotating disc composed of white dots (RDT) or on its own (RBT) on a black background. The rod was anti-aliased to smoothen its outline. Participants could rotate the rod around its centre in clockwise or counterclockwise directions using a keyboard's left and right arrow keys. The adjustment precision was 0.2°. A noisy black and white screen appeared for 2 s after each trial to avoid any residual image of the previous trial. Participants viewed the stimuli binocularly, wearing their usual visual equipment, at a distance of 60 cm. The tests were performed with the lights off in a black, window-less room. In addition, participants viewed the stimuli through a black 80 cm Ø tube, fixed onto an adjustable-in-height table, in order to avoid any peripheral visual cues. The table also served to align the centre of the rod with the participant's cyclopean eye.

The angular size of the frame (RFT), the disc (RDT) and the rod (RBT) were 28° of visual angle. For the RFT and RDT, the rod was slightly smaller, subtending 18.9° of visual angle. The frame and disc were

respectively tilted at 18° and rotated at 30°/s, clockwise (+) or counterclockwise (-) in order to produce a maximal visual perturbation effect (Bringoux et al., 2009; Dichgans, Held, Young, & Brandt, 1972; Zoccolotti, Antonucci, & Spinelli, 1993). The rod's initial orientation was +/- 18° in all three tests. The rod was tilted independently of the frame in the RFT and of the disc rotation direction in the RDT giving rise to four orientation combination conditions in each of the two tests. (For the RBT only two orientation conditions exist as the rod is the only stimulus).

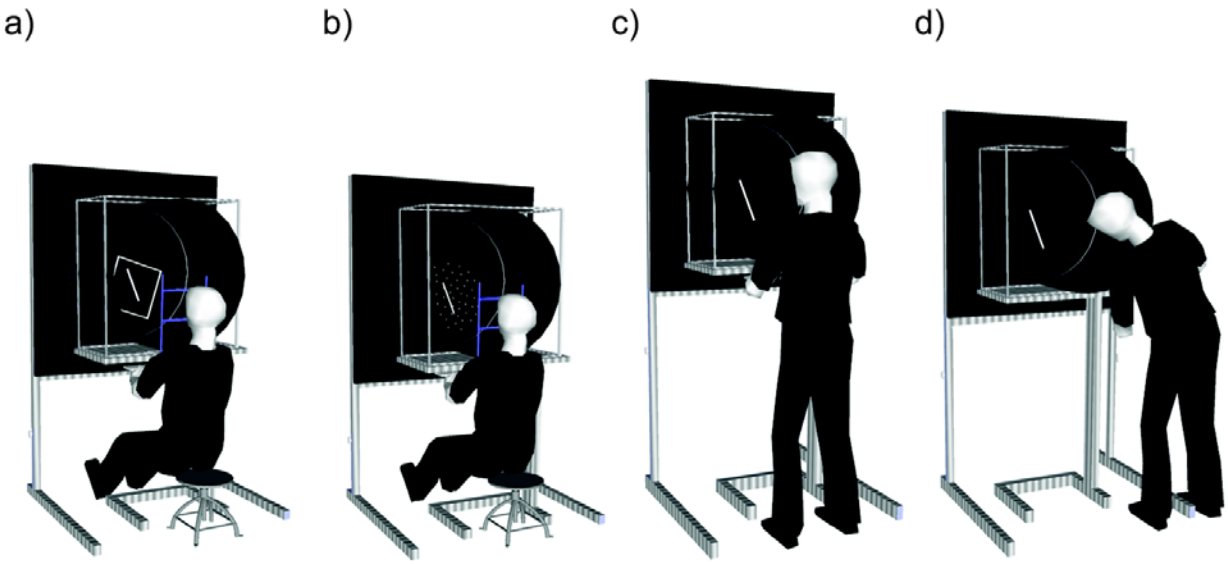

Figure II.1 : Illustration of apparatus, postural conditions and stimuli used for the subjective vertical estimation tests. Stimuli were back-projected onto a screen. A table, adjustable in height, held a black optic tube through which participants viewed the stimuli in order to reduce peripheral visual cues. For the Rod and Frame Test (RFT) **(a)** and Rod and Disc Test (RDT) **(b)** a head and chinrest was attached onto the table to keep the head fixed. Visual stimuli were a white tilted rod within a white tilted frame and within a disc of white dots for the two tests, respectively. The table was raised as appropriate for the Rod and Body Test during the Body Erect (RBT BE) **(c)** and Body Tilted (RBT BT) **(d)** postural conditions so as the centre of the rod was centered on participants' cyclopean eye.

For the RFT and RDT, a head and chinrest was fixed onto the table in order to keep the head vertical, and thus prevent the use of vestibular and somatosensory cues. In addition, participants sat at the edge of a stool, legs extended with only heels touching the ground in order to minimize somatosensory inputs from the rest of the body. For the RBT, participants stood upright with legs hip width apart, either with the body erect (BE) or with the body tilted (BT) at hip level, i.e. aligned or misaligned with gravity. For the BT condition, they were instructed to tilt their head and trunk laterally, so as to obtain an angle of 70° between the head and the vertical in order to ensure the production of an Aubert-, or A-Effect. The A-Effect denotes an underestimation of the body/vertical angle, which would be mainly of somatosensory origin (Anastasopoulos et al., 1999; Kaptein & Van Gisbergen, 2004; Yardley, 1990) whereby the perception of the vertical is attracted towards the body's Z axis. Due to the observed symmetry in subjective vertical estimation with

respect to tilt side (Van Beuzekom, Medendorp, & Van Gisbergen, 2001), participants were free to choose their preferred tilt side and kept it throughout the test. Visual controls were made using a protractor placed at the base of the skull to ensure the minimum angle between the head and the true vertical was obtained before each trial. Body tilt was maintained 10 s before each trial to familiarise with the body posture. At the end of each trial participants stood upright for 10 s to prevent fatigue. Figure II.1 illustrates the apparatus, postural conditions and stimuli used for the subjective vertical estimation tests.

Five trials were performed for each orientation condition in all subjective vertical estimation tests. A total of 20 trials for the RFT and for the RDT and 10 trials for the RBT were randomized within each test. Subjects were given no feedback about their performance. Error of subjective vertical estimation was scored in degrees of deviation from vertical. Mean absolute errors were calculated across trials and conditions for each test. Larger errors in subjective vertical estimation whilst perturbed by a tilted frame or rotating disc indicate greater visual field dependence. Greater egocentric dependence means that the somatosensory cues of body orientation have a bigger influence on subjective vertical estimation. Individuals with smaller errors with the body erect and larger errors when the body is tilted (greater A-Effect), therefore, rely on the egocentric frame of reference. The difference between errors in the BT and the BE condition was hence calculated and used in our analyses, larger values indicating greater egocentric dependence and reliance on somatosensory cues of body orientation for vertical estimation.

II.2.4 Visual fixation instability

Visual fixation instability (VFI) was assessed as a basic measure of oculomotor control. VFI was evaluated using the same apparatus as for visual field evaluation. The microperimeter has a spatial and temporal resolution of 0.1° and 25 Hz, respectively. Measurements were made monocularly for each eye, with the other one covered. Participants were instructed to fixate a centrally displayed cross during 30 s. Eye positions were recorded by tracking a retinal landmark and the data treated to remove blinks. VFI was quantified by calculating a bivariate contour ellipse area (BCEA, expressed in minarc^2) encompassing 68% of fixation points. The BCEA is the 2D analogue of standard deviation. Consequently, large BCEA values are an indication of greater fixation instability. Binocular BCEA was considered that of the better eye.

II.2.5 Useful field of view

All participants performed the Useful Field Of View Test (UFOV®; Visual Awareness Research Group, Inc). The UFOV is defined as the visual field area over which information can be acquired in a brief glance without eye or head movements. We used the three-subtest version of the test (Edwards et al., 2005). UFOV 1 required subjects to identify a central target presented in a fixation box. UFOV 2 assesses divided attention capabilities. It requires central target identification and simultaneous localisation of a peripheral target. UFOV 3 assesses selective attention capabilities. It includes the first two subtest tasks, only the peripheral target is embedded amongst 47 distracters. Peripheral targets were presented at 15° eccentricity for the UFOV 2 and UFOV 3 subtests. Participants performed the test in the dark, sitting at a distance of 35 cm from a 19' monitor. They wore their optimal refractive correction and MA and OA had an addition of +3.00 δ to avoid blurry vision due to accommodation loss. Measurements were made binocularly, the head was not fixed but participants were instructed not to move and keep their gaze on the fixation box. The subtests were presented in their respective order, UFOV 1, then UFOV 2 then UFOV 3. Five practice trials were preformed prior to each subtest. In each subtest, targets were presented at brief display durations (16.67 – 500 ms) following a double staircase protocol. The display duration at which each subtest can be performed accurately 75% of the time was measured. Thus scores for each subtest could range from 16.67 to 500 ms, indicating the visual processing speed associated to each task. We were interested in the UFOV 2 and 3 subtests as measures of peripheral visual processing ability and attention.

II.2.6 Data analysis

Statistical analysis

To evaluate age group effect, one-way analyses of variance (ANOVAs) were performed for all tests except for the UFOV where a 3 (age group) x 2 (subtest) repeated measures ANOVA was performed. The partial eta squared (η^2) was used to determine effect strengths. Tukey's honest significant difference (HSD) test ($p < 0.05$) was used for *post hoc* comparisons. Pearson correlations were performed between visual field dependence tests (RFT, RDT and GEFT) to certify that our measurements were robust with respect to the literature. Correlations were also used to evaluate the relationship between VFI, UFOV and measures of visual field and egocentric dependence. For all these simple linear correlations, we examined the sign of the regression equation and R^2 values were used to determine correlation strength, significance being $p < 0.01$.

II.3 Results

II.3.1 Control of visual and cognitive functions

Results of visual functions' measurements are summarised in Table II.1 for each age group. The visual field maps determined for each eye revealed no impairment in any of the participants. Although there was an age effect on visual acuity (F (2, 55) = 13.93, p = 0.000; η^2 = 0.34), it should be mentioned that the average visual acuity of the OA group was -0.12 logMAR (12/10), which is considered as good vision. The observed difference between the visual acuities of YA and OA is 0.1 logMAR, i.e. 1 line on the chart. We thus deemed this difference negligible in the context of our study. There were no significant differences between age groups on any of the other measures of visual function. The Mini Mental State Estimation was used to screen for cognitive frailty, all subjects achieved scores of 27 out of 30, or higher.

Table II.1: Summary of visual functions assessed for each age group

	Visual	Contrast	Titmus Stereotest	
Age Group	Acuity (logMAR)	Sensitivity (log)	Fly (mm)	Wirt Points (’’)
YA	-0.22 ± 0.07	1,97 ± 0.07	36 ± 9	41 ± 2
MA	-0.17 ± 0.06*	1,95 ± 0	38 ± 5	38 ± 28
OA	-0.12 ± 0.06*†	1.91 ± 0.12	34 ± 8	34 ± 48

*: significant difference with YA

†: significant difference with MA

II.3.2 Visual field dependence increases with age

Mean scores and standard deviations on the measures of visual field dependence, i.e. the GEFT, RFT and RDT, are summarised in Table II.2. Results confirm reports in the literature of increased visual field dependence with old age. The ANOVAs performed for each test revealed a significant main effect of age group (GEFT: F (2, 55) = 27.66, p = 0.000; η^2 = 0.50; RFT: F (2, 55) = 22.64, p = 0.000, η^2=0.45; RDT: F (2, 55) = 17.89, p = 0.000; η^2=0.39). *Post hoc* analysis for each test indicated a significant difference

between all age groups on the GEFT and RDT, and between YA and OA and between MA and OA on the RFT (p <0.05).

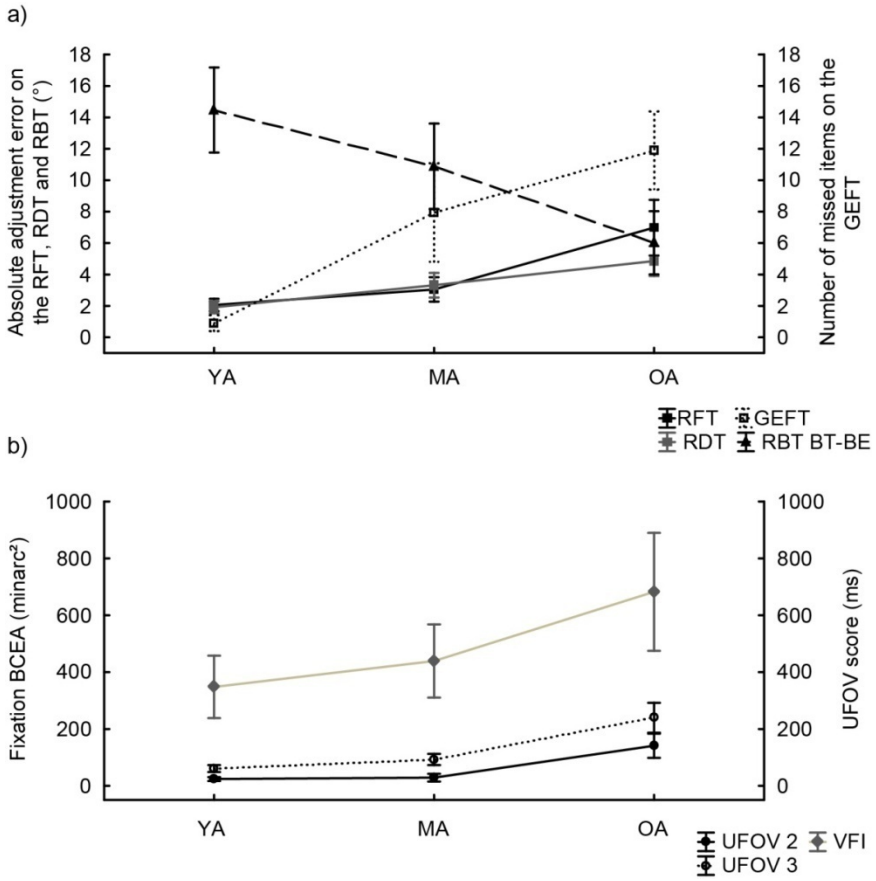

Figure II.2: Scores for each age group on all assessments - means with 95% confidence intervals. a) Adjustment error on the RFT and RDT, error difference between the RBT tests (BT – BE) and GEFT scores; b) Visual fixation bivariate contour ellipse area (BCEA) and UFOV 2 and UFOV 3. For the RFT, RDT and GEFT scores, larger mean values indicate greater visual field dependence. For RBT data, larger mean values indicate greater egocentric dependence. For VFI and UFOV data, larger values indicate greater visual fixation instability and longer processing times (reduced UFOV), respectively.

II.3.3 Egocentric dependence decreases with age

Mean scores and standard deviations of absolute error on the RBT BE, RBT BT and mean difference between BT and BE errors for each age group are also presented in Table II.2. In this test, only body orientation can provide information for spatial orientation, therefore, larger errors in the BE condition, and smaller errors in the BT condition (reduced A-effect) reveal a misjudgment of body orientation perception. The ANOVA performed on the difference of errors revealed a significant age group effect (F (2, 55) = 13.24,

p = 0.000; η^2= 0. 33). Post hoc analysis indicated a significantly lower reliance on the egocentric frame of reference for the OA compared to YA and MA (p <0.05).

II.3.4 Relationship between visual field and egocentric dependence

Mean errors on each test of visual field and egocentric dependence are presented in Figure II.2a. Prior to examining the contribution of egocentric referencing on reliance on visual field dependence, we ensured the robustness of the link between the standard visual field dependence tests, i.e. RFT, RDT and GEFT, with respect to the literature. We observed that larger errors on the RFT correlated positively with larger errors on the RDT (R^2 = 0.51, p = 0.000). Similarly, significant positive correlations were found between the GEFT scores and RFT (R^2 = 0.40, p = 0.000) as well as RDT (R^2 = 0.56, p = 0.000). The respective strengths of these relationships are consistent with the literature (Isableu et al., 1998; Wachtel, 1972).

We subsequently performed correlation analyses between the RBT and all visual field dependence tests. Significant negative correlations were found between the RBT and RFT (R^2 = 0.28, p = 0.000), RDT (R^2 = 0.33, p = 0.000) and GEFT (R^2 = 0. 32, p = 0.000), indicating that increased visual field dependence is linked to reduced reliance on the egocentric frame of reference.

Table II.2: Summary of Visual Field and Egocentric Dependence Tests for each age group

				RBT Absolute Error (°)		
Age Group	**GEFT (number of missed items)**	**RFT Absolute Error (°)**	**RDT Absolute Error (°)**	***BE*[1]**	***BT*[1]**	***BT-BE***
YA	1 ± 1	2.1 ± 0.8	1.9 ± 0.8	1.1 ± 0.6	15.5 ± 5.7	14.5 ± 5.8
MA	8 ± 6*	3.0 ± 1.6	3.3 ± 1.6*	1.7 ± 0.8	12.6 ± 5.5	10.9 ±5.5
OA	12 ± 5*†	7.0 ± 3.8*†	4.9 ± 2.0*†	1.9 ± 1.9*	8.5 ± 3.2*	6.0 ± 4.3*†

*: significant difference with YA
†: significant difference with MA

[1] A 3(age group) x 2(postural condition) repeated measures ANOVA was performed on z-scores (to account for scale differences) of the RBT BE and BT adjustment errors. Tukey's HSD on the posture*age group interaction (F(2, 55) = 14.27, p = 0.000, η^2 = 0.34) revealed the significant differences presented

II.3.5 Visual fixation instability and useful field of view

VFI and UFOV mean scores and standard deviations are summarized in Table III.3 and illustrated in Figure II.2b. A one-way ANOVA revealed a significant age group effect on fixation BCEAs (F (2, 55) = 5.54, p = 0.006; η^2= 0.17). *Post hoc* analysis indicated that OA present significantly larger BCEAs, i.e. a larger fixation area compared to YA (p <0.05). In addition, with the repeated measures ANOVA on UFOV 2 and UFOV 3, we found significant effects of age group (F (2, 55) = 48.63, p = 0.000; η^2= 0.64), subtest (F (1, 55) = 43.85, p = 0.000; η^2= 0.44) and the interaction group*subtest (F (2, 55) = 3.28, p = 0.045; η^2= 0.11). OA required significantly longer processing speeds compared to YA and MA for each test (p <0.05). We observed positive correlations between VFI and UFOV 2 (R^2 = 0.23, p = 0.000) and UFOV 3 (R^2 = 0.15, p = 0.003), i.e. as fixation area increases, so does the display duration necessary in order to complete each attention task in the UFOV test.

Table II.3: Summary of Visual fixation Instability (VFI) and Useful Field Of View (UFOV) assessment for each age group.

Age Group	Fixation BCEA (minarc²)	UFOV 1 (ms)	UFOV 2 (ms)	UFOV 3 (ms)
YA	347.91 ± 234.47	16.9 ± 0.7	23.9 ± 14.3	60.7 ± 26.2
MA	438.93 ± 258.76	16.7 ± 0	28.6 ± 27.5	92.8 ± 39.7
OA	682.46 ± 443.46*	25.4 ± 25.1	140.8 ± 91.0*†	239.5 ± 111.9*†

*: significant difference with YA
†: significant difference with MA

II.3.6 Correlations between measures of visual and egocentric dependence with visual fixation stability and useful field of view

We ultimately analyzed visual field and egocentric dependence tests with respect to VFI and UFOV. We explored the relationship of visual fixation instability and spatial orientation (both visual and egocentric referencing) by correlating VFI with all subjective vertical estimation tasks. As illustrated in Figure II.3, significant correlations were found, positive between VFI and both RFT (R^2 = 0.28, p = 0.000) and RDT (R^2 = 0.25, p = 0.000), and negative between VFI and RBT (R^2 = 0.20, p = 0.000). Finally, in order to understand the effect of peripheral visual information attention and processing deficits on reliance on the visual frame of reference UFOV 2 and UFOV 3 were correlated with measures of visual field dependence (Figure II.4). GEFT performance correlated positively and significantly with both UFOV 2 (R^2 = 0.30, p = 0.000) and

UFOV 3 (R^2 = 0.36, p = 0.000). The trend was similar for the positive correlations between the RFT and UFOV 2 (R^2 = 0.39, p = 0.000) and UFOV 3 (R^2 = 0.36, p = 0.000), as well as between the RDT and UFOV 2 (R^2 = 0.20, p = 0.000) and UFOV 3 (R^2 = 0.27, p = 0.000).

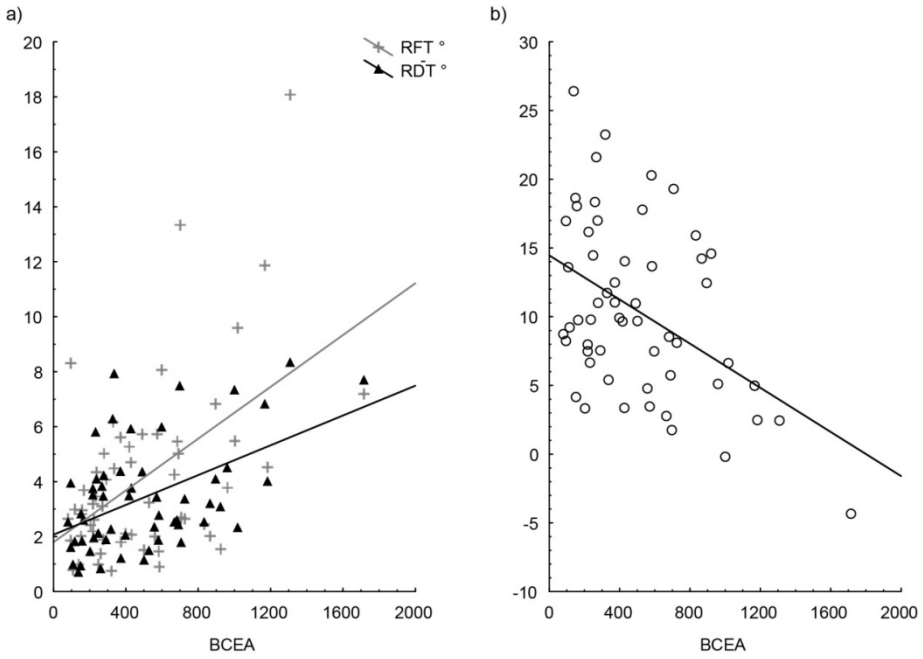

Figure II.3 : Relationship of Visual Fixation Instability (VFI) with subjective vertical estimation tests. a) VFI correlation with the RFT and the RDT b) VFI correlation with the RBT (BT – BE error).

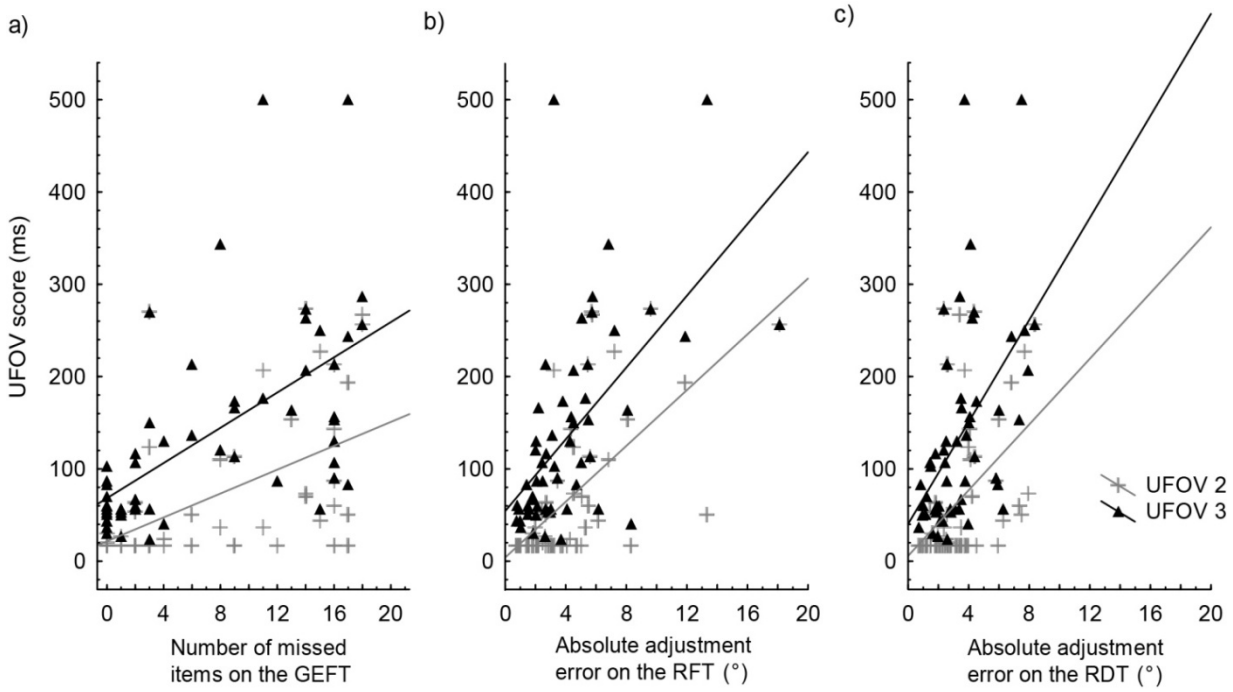

Figure II.4 : Relationship of Useful Field Of View (UFOV) subtests 2 and 3 with visual field dependence tests. a) UFOV 2 and 3 correlations with the GEFT b) UFOV 2 and 3 correlations with the RFT c) UFOV 2 and 3 correlations with the RDT.

II.4 Discussion

The current study explored possible factors contributing to visual field dependence in old age by evaluating egocentric dependence, visual fixation instability (VFI) and useful field of view (UFOV) across adulthood. To our knowledge, this is the first cross-sectional study examining these parameters as well as their inter-relationships in the context of ageing. We performed a battery of spatial orientation, oculomotor and cognitive tests on a sample population of young, middle-aged, and old adults. We proceed to discuss results in terms of frame of reference selection with respect to ageing as this implies processing of visual and non-visual orientation, position and motion cues for perceptual and interactive sensorimotor tasks of daily living. We shall also emphasize the significance of middle-aged adults' data in terms of frame of reference shifting with age and conclude with future perspectives in this field of research.

II.4.1 Age effect on frame of reference selection

We performed three tests of visual field dependence and an assessment of egocentric dependence in all three age groups. Taken together, results of these assessments reveal that not only do individuals show greater reliance on the visual frame of reference with age, but that this process is accompanied by a lower reliance on the egocentric frame of reference. Scores on the RFT, RDT and GEFT (Table II.2) confirmed the age-related increase in visual field dependence reported in the literature (Eikema et al., 2012; Kobayashi et al., 2002; Matheson, Darlington, & Smith, 1998; Panek et al., 1978; Schwatz & Karp, 1967; Slaboda et al., 2011). In agreement with studies examining egocentric referencing in old adults (Barbieri et al., 2010; Schwatz & Karp, 1967), we found egocentric dependence decreasing with age (Table II.2). This is evidenced in old adults by larger adjustment errors in the RBT body erect (BE) postural condition, but mainly, by smaller errors in the body tilt (BT) condition, i.e. a reduction of the somatosensory-based A-effect. Our study is the first investigation, to our knowledge, revealing a reduction of the A-effect in the frontal plane with age, but more importantly the first directly linking an increase of visual with a decrease of egocentric reference frame reliance.

The positive correlation between UFOV and scores on the RFT, RDT and GEFT (Figure II.4) confirm the role of visuospatial as well as divided and selective attention in visual field dependence (Goodenough et al., 1987; Yan, 2010). It is well known that UFOV decreases with age, revealing reduced speed of information processing, inability to ignore distracters and inability to divide attention (Owsley, Ball, Sloane, Roenker, & Bruni, 1991). Our data agree with studies of psychological differentiation attributing visual field independence with resistance to distraction (Bednarek & Orzechowski, 2008). These authors point out that visual field independence (analytic reality perception) may imply efficient functioning of selective attention

whereas visual field dependent individuals have less efficient attention mechanisms, which reduce stimulation (thus reinforcing specific cognitive preferences). Other studies have also reported declines in cognitive processes in old adults, including slower information processing (Salthouse, 2000) and reduced visual attention inhibition (Connelly & Hasher, 1993; Sweeney, Rosano, Berman, & Luna, 2001). Our results support the hypothesis that increased visual field dependence with age relates to both sensory and cognitive decline. In addition, UFOV assessment is associated with driving cessation, unsafe driving and crash risk amongst old adults as it implies both visual sensory abilities and higher order attentional skills for old adults (Ball et al., 1993; Ball et al., 2006; Goode et al., 1998; Mathias & Lucas, 2009; Owsley et al., 1991; Owsley et al., 1998; Wood, Chaparro, Lacherez, & Hickson, 2012)– although there is some ambiguity with respect to the UFOV test's validity as a predictor of safe driving (Aksan et al., 2012; Emerson et al., 2012). Our data are in agreement with older studies relating perceptual style and selective attention/visual search in the context of driving performance and crash risk (Guerrier et al., 1999; McKnight & McKnight, 1999; Mihal & Barrett, 1976). Indeed, Barrett & Thornton (Barrett & Thornton, 1968) have pointed out that visual field dependence and automobile accident involvement show similar trends with age.

The inter-individual variability in visual field dependence amongst old adults should be pointed out. In our study, greater visual field dependence is associated with reduced ability to exploit somatosensory information, visual fixation stability, and useful field of view. Moreover, inter-individual variability of VFI and UFOV was larger amongst old adults than within the other age groups (Table II.3). Studies have shown that more visual field dependent old adults are at higher risk of falls (Lord & Webster, 1990) and that sedentary old adults are also more visual field dependent than their more active age- and education- matched counterparts (Karp, 1967; Markus & Nielsen, 1973; Rotella & Bunker, 1978). The ageing factor may thus give a different dimension to visual field dependence/independence. Greater visual field dependence amongst old adults may signify an *over-reliance* on visual information, regardless of the appropriateness of using the visual frame of reference, i.e. visual cues are consistently considered more reliable than non-visual existent cues. We hypothesize that age-related deficits may induce this over-reliance on visual information in more affected old adults. The literature makes no distinction between visual field dependence due to vicariance and visual field dependence due to age-related deficits as sensory and cognitive processes are either not examined or not investigated with respect to spatial orientation. However, it is important to distinguish the two cases. The latter would mean that not only is shifting reliance from the visual to another, more appropriate frame of reference more difficult (Bugnariu & Fung, 2007; Eikema et al., 2012; Eikema et al., 2013; Slaboda et al., 2011; Slaboda & Keshner, 2012), but also that the visual frame of reference is not exploited in an optimal manner due to age effects. The correlations between visual field dependence and the other assessments support this idea: on the one hand, reduced visual fixation stability and useful field of view affect how visual information is perceived and processed; on the other, the diminished attention capacity (measured through the UFOV test) and reliability of egocentric cues (revealed via the RBT and weakened oculomotor control in the fixation task) make it more difficult to dynamically switch from one reference frame to another.

II.4.2 Proprioceptive neglect within the profile of visual field dependence

Preferential selection of the visual as opposed to the egocentric frame of reference may be linked to a neglect of sorts, or difficulty to integrate the sensory inputs tied to the egocentric frame of reference in old adults. In adults as well as in adolescents (Isableu et al., 2003; Viel, Vaugoyeau, & Assaiante, 2009), this neglect appears to correspond to a difficulty in integrating proprioceptive inputs and allocating attentional sensorimotor resources to coordinate systems of non-visual frames of reference. The RBT scores revealed that old adults (and to a lesser degree middle-aged adults, but still more than young adults) have trouble exploiting body-based inputs in the absence of visual information. The subjective vertical cannot be built without the mediation of the egocentric perception of one's body position relative to gravity (Anastasopoulos et al., 1999; Luyat, Ohlmann, & Barraud, 1997; Mittelstaedt, 1983; Yardley, 1990). This leads us to consider that the Z body axis does not provide salient enough information for old adults. More specifically, somatosensation is known to contribute to the sense of verticality (Barbieri et al., 2008) and be affected by age (Shaffer & Harrison, 2007). The somatosensory origin of the A-effect has been established by observing the systematic disappearance of the A-effect depending on the body region and extent of somatosensory neglect in deafferented (Yardley, 1990), hemiaesthetic and paraplegic patients (Anastasopoulos et al., 1999; Barra et al., 2010). We therefore infer that the somatosensory contribution for spatial orientation is reduced with age. Moreover, somatosensory information processing requires the integration of signals from all the joints and muscles involved in a given movement or posture maintenance. Such information processing is therefore more complex for old adults as it increases the demand of attentional resources.

Contrary to older reports (Crossland et al., 2008; Kosnik et al., 1987; Shallo-Hoffmann et al., 1990), we observed greater oculomotor instability in the old adult group while fixating a target. Studies have shown that extra-retinal signals provide afferent and efferent input contributing to gaze direction information (Roll, Velay, & Roll, 1991), spatial orientation (Lewald & Ehrenstein, 2000), the control of posture (Guerraz & Bronstein, 2008; Kapoula & Lê, 2006; Roll & Roll, 1988; Strupp et al., 2003; Wolsley, Sakellari, & Bronstein, 1996) and locomotion (Royden, Banks, & Crowell, 1992). Indeed, these inputs are linked to the neck and ankle proprioceptive signals, thus participating in a 'proprioceptive chain' (Roll & Roll, 1988). The positive correlation we found between decreased visual fixation stability and egocentric dependence (Figure II.3b) is consistent with these studies, which ultimately suggest that extra-retinal information contributes to the construction of a body reference system (Roll, Vedel, & Roll, 1989). We suggest that visual fixation instability adds noise to the chain of body proprioceptive information. In addition visual fixation instability was also positively correlated with greater visual field dependence (Figure II.3a).

Taken together, our results support the concept of proprioceptive neglect, or more generally, neglect of somatosensory input, as a main cause of over-reliance on visual frame of reference and increased visual field dependence in old adults. Somatosensory inputs convey noise, while age effects on higher-order capacities

render the processing of proprioceptive-chain information more uncertain. Reliance on the visual frame of reference is thus reinforced, as, in comparison, visual input is considered less ambiguous.

II.4.3 Peripheral visual information and visual field dependence

For the RFT and RDT tasks, one must ignore peripheral visual information (the tilted frame and rotating disc) in order to accurately align the rod to vertical. In the UFOV 2 and 3 subtests, the scores depend on the individuals' capacity to accurately identify elements in both central and peripheral visual fields (and inhibit distracters in UFOV3). At first view, there would appear to be a certain paradox in that individuals who take into account the peripheral visual information for spatial orientation (visual field dependent) are also those who have difficulty processing peripheral visual information in the UFOV tests. Our correlations of visual field dependence tests to the two UFOV subtests (Figure II.4) imply that for more visual field dependent participants, peripheral visual information is not only disorienting, as it adds information that is hard to ignore, but also distracting, as it adds noise. It is important, however, to highlight the very short timescale of the UFOV test. Whilst it is reasonable to deduce that peripheral visual information processing is negatively affected by ageing, the limited display duration on the UFOV test, is a moderating factor on such a statement as various higher order processes come into play. Furthermore, it should be pointed out, that UFOV 3 is not only a test assessing inhibition of distracters, attention and processing in the *peripheral* visual field, but is in itself also a more difficult, cognitively demanding task. Research has revealed visual processing impairments in old adults when attentional load is increased in *central* tasks as well (Russell, Malhotra, Deidda, & Husain, 2013). It should be noted therefore that, with age, cognitive load affects perception in a general manner. The UFOV 2 and 3 subtests may be paralleled to dual tasks, with concurrent exercises in the central and peripheral visual fields. Given the limited timescale, older and more visual field dependent perceivers prioritize the central over the peripheral task. The higher display durations required, however, to accomplish the UFOV subtests reveals that these participants are sensitive to peripheral visual cues, taking them into account nevertheless, just as in the visual field dependence test paradigms. Studies examining coordination strategies for segmental stabilisation have also shown that visual field dependent individuals are more sensitive to peripheral visual cues for both static (Isableu et al., 2010; Isableu et al., 1998) and dynamic (Assaiante & Amblard, 1992; Assaiante & Amblard, 1993) balance. The shared variance between visual field dependence and UFOV thus supports the fact that these tests examine both temporal and spatial visual processing ability in addition to attention capacity. These functions are particularly relevant for old adults' daily living tasks and sensorimotor control in general in order to preserve autonomy.

Patients with peripheral field loss increase their eye movements to obtain more samples of their limited visual environment (Li, Peli, & Warren, 2002). During visual search, old adults make more (Scialfa et al., 1994) as well as illicit (Beurskens & Bock, 2012) saccades to compensate UFOV shrinkage. Considering

such oculomotor consequences of limiting peripheral visual information processing, we may suggest that visual fixation instability (which implies fine control of very small movements) may indeed be partly attributed to UFOV reduction with age. The alternative hypothesis, however, may also be valid, positing that visual fixation instability may actually lead to a reduction of the UFOV. Since visual fixation instability affects peripheral visual information perception as well (Macedo et al., 2008; Murakami, Kitaoka, & Ashida, 2006), VFI due to age could engender reduced peripheral information processing capacities, thus shrinking the UFOV. Taking together the correlations of visual fixation instability with both UFOV and visual field dependence, we may suggest that visual fixation instability is linked to greater reliance on the visual frame of reference not only in terms of noisy extra-retinal input (as discussed further above), but also in terms of the noisy visual input it implies.

II.4.4 Middle-aged group: evidence of progressive shift in reference frame selection

Given the implications of greater reliance on the visual frame of reference of old adults mentioned in the above sections, examining possible associated sensorimotor and/or cognitive factors across adulthood can help illuminate the process of this shift in reference frame selection with age. Seeing as we did not obtain an even distribution of ages in our population sample from young to old adults, correlations were not performed with respect to age, but ANOVAs with respect to age groups. Trends revealed the middle-aged adult group responses on all assessments as falling between those of young and old adults, as seen in Figure II.2. Our results cannot argue in favour of linear or non-linear change with age, but this is outside the scope of our study. What our data do suggest, however, is that inter-individual variability increases in middle-age and onto old age and that cognitive and sensorimotor decline does not occur ‘out of the blue’ past a certain age. Indeed, certain cognitive functions are known to decline by middle-age (Salthouse, 2009), as does sensory/sensorimotor performance when additional attentional resources are required (Jamet, Deviterne, Gauchard, Vancon, & Perrin, 2007; Lindenberger, Marsiske, & Baltes, 2000; Sekuler et al., 2000). More importantly, we have further evidence that visual field dependence increases from young to middle-aged adulthood. The correlations we found with egocentric dependence, visual fixation instability and UFOV show that these factors, also evolving with age, contribute to a certain extent towards this shift in reference frame selection. *Post hoc* analysis of our data revealed significant differences between all three age groups only on the GEFT and RDT (Table II.2). Lee & Pollack (1980) suggest that in middle-age, there is evidence of perceptual-cognitive issues that lead to greater visual field dependence with old age. In addition, dynamic visual stimuli have been shown to be more discriminating than static ones between fallers and non fallers amongst old adults (Lord & Webster, 1990). It could be that sensitivity to dynamic visual cues (in addition to cognitive capacity mentioned above) is more prone to ageing effects.

It should also be mentioned that studies involving visual tasks may obtain biased results for middle-aged adults due to the increased distance required for accommodation caused by the onset of presbyopia (Sekuler

et al., 2000), thus revealing more old-adult-like behavior. In the current study, we controlled for this by providing trial frames with increased lens additions to middle-aged and old adults according to the distance of our visual examinations, notably, for the UFOV assessment.

II.4.5 Limitations of our experiments and future perspectives

A critical appraisal of our study must consider the relative strengths of certain correlations. It should be pointed out that we explain only part of the variance of each test as related to visual field dependence/independence. It is this shared variance, however, that is systematically found in sensorimotor control – field dependence/independence correlations, which can affect the adaptation capability of individuals to select and appropriately shift their reliance on different frames of reference (Isableu et al., 2010; Isableu et al., 1998; Slaboda & Keshner, 2012). The unevenness in our correlations is also due to important inter-individual variability in test responses. In particular for visual fixation instability and useful field of view, variability was high between participants (especially amongst old adults, see Table II.3).Variability in UFOV scores has been previously reported in the literature (Edwards et al., 2006). With this in mind, the substantial inter-individual variability warrants caution when generalising the statement that UFOV degrades with age, even though this decline is significant. Moreover, Beurskens & Bock (2012) suggest UFOV reduction with age is due to central declines. It is possible that cognitive capacities differed amongst our old adult participants (these differences being too fine to be identified via the MMSE cognitive control test). We have already reported the important implication of central processing mechanisms within the profile of visual field dependence. Had we obtained a larger population of old adults, a clustering analysis may have allowed us to partition participants and revealed to a greater degree the association between increased visual field dependence between old adults and reduced UFOV and visual fixation stability. It is also important to be cautious when interpreting correlations between visual field dependence tests and other measures as the shared variance between a test of visual field dependence and the separate variable may not be the same as that shared between different measures of visual field dependence (Wachtel, 1972). However, we can have confidence in our results given that the examined variables correlated significantly to all three of our visual dependence tests (GEFT, RFT and RDT).

Finally, our study has uncovered a reduction in the visual processing and somatosensory contributions to increased visual field dependence with age which may be taken into account in future intervention programs for frailer old adults. We would like to highlight that although it has been established that rigid reliance on the visual frame of reference is a risk factor for old adults, this spatial referencing shift need not be perilous. The main issue of increased visual field dependence is the implication of reduced adaptive and attentional capacities, both of which may be improved with appropriate training. Sensory reweighting (and ultimately learning to identify and utilise more appropriate frames of reference with respect to task constraints) has been shown to improve with time and/or practice in both young (Brady et al., 2012) and old adults (Doumas

& Krampe, 2010; Eikema et al., 2013; Jeka et al., 2006), while physical activity in general ameliorates both cognitive and physical capabilities affected by age (Seidler et al., 2010) and, in particular, preserves visuospatial functions (Shay & Roth, 1992). Furthermore, taking visual field dependence into account in rehabilitation programs for sedentary old adults can lead to optimizing the use of the visual frame of reference, rendering visual field dependence more functional - as is done for young adults (Yan, 2010) and Parkinson's patients (Azulay, Mesure, & Blin, 2006). This can also be done by improving the functionality of factors associated with visual field dependence. Visual fixation stability (Kosnik, Fikre, & Sekuler, 1986), divided and selective attention (Ball, Beard, Roenker, Miller, & Griggs, 1988; Richards, Bennett, & Sekuler, 2006; Sekuler & Ball, 1986) and processing of complex dynamic scenes (Legault, Allard, & Faubert, 2013) can be increased with training. Egocentric referencing may also be boosted and thus reduce the perpetual higher weight of visual input, by improving vestibular and somatosensory acuity with appropriate practice (Gauchard, Jeandel, & Perrin, 2001; Pavlou et al., 2011; Verschueren, Brumagne, Swinnen, & Cordo, 2002). It is important therefore to be able to distinguish reliance on the visual frame of reference as a preferred spatial referencing mode or as a constraint associated with other age-affected factors in old adults. Training programs for the latter group would thus serve not only to reduce the noise associated with non-visual (or confounding visual) cues but also improve old adults' capacity to distinguish exploitable signal from noise in all available sensory information.

II.5 Conclusion

Our results confirm literature reports of greater visual field dependence with age and show a progressive increase from young, to middle-aged, to old adulthood. In addition all three factors examined revealed a degradation occurring with age: in the exploitation of the egocentric FoR, in parallel visual attentional processing ability and in visual fixation stability. Importantly, these reductions with age were associated with increased reliance on the visual FoR. We noted the possible somatosensory degradation due to age as inferred from the reduced RBT scores and visual fixation stability in old adults and that visual field dependence may thus lead to a form of neglect of such sensory signals. Notable was also the larger inter-individual variability observed amongst old adults. We suggest that greater reliance on the visual FoR amongst old adults may signify a default (compensatory) rather than a preferred mode of spatial referencing given that the deficits occurring with age render visual information less reliable but also the shift to exploit a more appropriate FoR more difficult. We suggest reliance on the visual FoR be taken into account when designing rehabilitation and training protocols for frailer old adults. The distinction as to whether this reliance is functional or compensatory in nature should also be made in order to provide more personalised care for the maintenance/recovery of autonomy.

III. *Chapter 3: Ground optic flow influence while standing and stepping in place across aging: reference frame reliance for self-motion perception*

Our second experimental chapter examined how age and reliance on the visual frame affected the influence of ground optic flow stimuli on self-motion perception while standing quietly or stepping in place. We projected approaching and receding optic flow stimuli on the ground surface given that it bears special ecological importance as a reference. Our aim was to determine to what extent our participants would rely upon visual, as opposed to somatosensory cues for self-motion perception, in the context of age and individual differences in reference frame reliance. We chose to study stepping in place in addition to quiet stance in order to examine whether the intermittent podal contact with the ground surface would lead to a greater optic flow effect. We hypothesised that old and more visual field dependent participants would show greater reliance on ground optic flow while stepping in place given their reduced reliance on the egocentric FoR established in the previous chapter.

An abbridged version of this chapter is under revision for submission to Neuroscience.

Agathos, C. P., Bernardin, D., Baranton, K., Assaiante, C., & Isableu, B. Drifting while stepping in place in old adults: association of self-motion perception with reference frame reliance and ground optic flow sensitivity

III.1 Introduction

Self-motion perception is important for interacting with one's environment, whether this be simply for maintaining postural balance, walking or performing more complex tasks such as intercepting a moving object and interacting in daily life. The optic flow due to body motion provides a visual affordance which serves to perceive the direction (heading) and speed of self-motion and thus to control the body during locomotion (Warren, Morris, & Kalish, 1988; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). In ecological situations, forwards or backwards movements of the body elicit approaching or receding flow respectively, corresponding to changes of the structured pattern of light on the retina. When the movement is initiated by an individual his or her eye and head movements are superimposed on body movements resulting in a mixture of anteroposterior, mediolateral and vertical displacements in addition to rotational components. The resulting optic flow specifies, along with efference copies, that the movements perceived are self-initiated and not externally induced. Optic flow has been shown to modulate gait (Pailhous, Ferrandez, Flückiger, &

Baumberger, 1990; Prokop, Schubert, & Berger, 1997) and induce postural reactions as well as illusions of self-motion (vection) in stationary individuals (Flückiger & Baumberger, 1988). In our study, we examined how the directional effects of linear ground optic flow on posture may be dependent on aging. More specifically, we were interested purely in the translational component of body motion. For this we analysed head, trunk and centre of pressure (COP) kinematics and head and trunk pitch orientation during quiet standing and stepping in place in young, middle-aged and old adults.

When walking, simulated optic flow affects gait kinematics and heading direction (Bardy, Baumberger, Flückiger, & Laurent, 1992; Chou et al., 2009; Mohler, Thompson, Creem-Regehr, Pick Jr, & Warren Jr, 2007; Prokop, Schubert, & Berger, 1997; Pailhous, Ferrandez, Flückiger, & Baumberger, 1990; Berard, Fung, McFadyen, & Lamontagne, 2009). The locomotor response to optic flow follows the perception-action relationship of natural walking. For example, approaching flow induces a decrease in walking speed due to the perception of faster self-motion (Baumberger, Flückiger, & Roland, 2000; François, Morice, Bootsma, & Montagne, 2011; Konczak, 1994; Prokop et al., 1997). Although receding flows are not common, nor are they ecologic when moving forwards, an underestimation of self-motion speed arises should the visual information be considered credible. Indeed, some studies report an increase in walking speed when faced with receding flows (Baumberger et al., 2000; De Smet, Malcolm, Lenoir, Segers, & De Clercq, 2009; Prokop et al., 1997). When an individual faces an optic flow-type stimulus while standing still, increased postural sway amplitude and variability with respect to natural conditions has been observed (Baumberger, Isableu, & Flückiger, 2004; Holten, Donker, Verstraten, & van der Smagt, 2013; Lestienne, Soechting, & Berthoz, 1977; Bronstein, 1986; Sundermier, Woollacott, Jensen, & Moore, 1996; Palmisano, Pinniger, Ash, & Steele, 2009; Wei, Stevenson, & Körding, 2010; Berthoz, Lacour, Soechting, & Vidal, 1979). Postural sway responses occur in order to counter perceived self-motion, with approaching flow ‘pushing’ perceivers back and receding flow ‘pulling’ them forwards (Flückiger & Baumberger, 1988). However, a few studies have observed an adaptation to the visual stimulus in adults whereby postural reactions occur in the opposite direction of the optic flow (Baumberger, Isableu, & Flückiger, 2004; Bronstein, 1986).

There is some inconsistency in the literature regarding age differences in postural responses when only dynamic visual cues from optic flow are manipulated, as opposed to somatosensory or vestibular cues. Some studies have revealed no difference in optic flow effects between young and old adults, both in stance (Bugnariu & Fung, 2007; Teasdale et al., 1991) and walking (Chou et al., 2009; Konczak, 1994; Schubert, Prokop, Brocke, & Berger, 2005). Others report a greater perturbation effect in old adults in stance (Borger et al., 1999; O'Connor et al., 2008; Sparto et al., 2006; Sundermier et al., 1996; Wade et al., 1995) and a reduced ability to exploit heading information (Berard, Fung, McFadyen, & Lamontagne, 2009; Warren, Blackwell, & Morris, 1989). However, studies do agree that old adults are more destabilised under concurrent visual and somatosensory perturbation and have slower or reduced sensory reweighting capacities (Borger et al., 1999; Hay, Bard, Fleury, & Teasdale, 1996; O'Connor et al., 2008; Simoneau et al., 1999;

Slaboda, Lauer, & Keshner, 2011; Sparto et al., 2006; Teasdale, Stelmach, Breunig, & Meeuwsen, 1991; Teasdale et al., 1991).

Somatosensory (such as proprioreceptive, cutaneous and efference copy signals), visual and vestibular sensory integration and reweighing are essential in order to adapt motor strategies to fulfil perception-action relationships. Moreover, the ability to perceive and control one's spatial orientation is based on the functional alignment of body axes (Fourre et al., 2009; Isableu et al., 2009; Isableu et al., 2010; Kluzik et al., 2005) either on directions within a gravito-inertial field or on surrogates of the direction of gravity such as axes within the visual frame of reference. The ground surface bears special ecological relevance as it is considered an invariant source of information, i.e. a reference, for postural control (Gibson, 1950). The ecological significance of visual information from the ground surface has been demonstrated in terms of greater processing efficiency by the visual system (Flückiger & Baumberger, 1988), as a reference for the perception of 3D layout (Bian, Braunstein, & Andersen, 2005) as well as offering an advantage in visual tasks such as apparent motion perception (Osaka, 1993) and visual search (Mccarley & He, 2000). In addition, somatosensory information from the ground surface is crucial in the maintenance of stance and for providing a stable reference. This has been evidenced by postural orientation and stepping adaptations to surface inclination (Kluzik et al., 2005; Kluzik, Peterka, & Horak, 2007; Gurfinkel, Ivanenko, Levik, & Babakova, 1995), rotation (Weber, Fletcher, Gordon, Jones, & Block, 1998) and translation (Anstis, 1995).

Depending on the task-specific inertial acceleration constraints and demands, axes of the body's different coordinate systems can be advantageously exploited, each in association with distinct frames of reference (Fourre et al., 2009; Guerraz, Poquin, Luyat, & Ohlmann, 1998; Guerraz, Poquin, & Ohlmann, 1998; Guerraz, Luyat, Poquin, & Ohlmann, 2000; Pagano & Turvey, 1995). Individual differences have been demonstrated in reference frame selection for certain spatial tasks indicating the existence of 'perceptual-motor styles' whereby an individual expresses a stable preference over time to exploit one mode of spatial referencing among others. Reliance on the visual reference frame in young adults has been linked to greater postural reactions under simultaneous visual and somatosensory perturbation, and reduced reweighting ability (Slaboda & Keshner, 2012; Brady et al., 2012; Isableu et al., 2010; Slaboda et al., 2011; Slaboda & Keshner, 2012; Isableu et al., 2011). Furthermore, it has been reported that reliance on the visual frame of reference increases in old age (Agathos et al., 2015; Straube et al., 1988; Sundermier et al., 1996). Indeed greater reliance on the visual reference frame has been demonstrated in old adults showing difficulties in dynamic sensory reweighting, suggesting that old adults utilise visual rather than somatosensory-based egocentric modes of spatial referencing (Eikema et al., 2012; Slaboda et al., 2011).

In our study, we wanted to characterise this age–related increased reliance on visual information with possible associated motor signatures. Specifically, we were interested in whether and how ground optic flow perception affects motor behaviour with aging and whether this effect is enhanced when the podal contact with the ground surface becomes intermittent by the act of stepping in place. Stance and walking differ in the nature of perturbations to postural control and the sensorimotor mechanisms used to maintain orientation and

equilibrium. When walking the gravito-inertial force sensed by the vestibular system is more prominent, as is the optic flow generated by the body's forward motion, sway and bounce. In addition, the intermittent podal contact means that the body-on-support surface information relayed by the somatosensory system is not a constant reference. Moreover, a certain amount of noise is conveyed in the somatosensory signal due to the shock associated with each foot contact on the ground. Altering the pattern of gravito-inertial information and availability of podal support surface information may therefore affect egocentric perception of the body relative to the ground. To examine this, we used a new paradigm whereby participants stepped in place under different conditions of optic flow. Stepping in place, has been shown to lead to similar head orientation strategies as during actual walking (Pozzo, Berthoz, & Lefort, 1990; Hirasaki, Kubo, Nozawa, Matano, & Matsunaga, 1993). In the present study, we investigated postural responses in the anteroposterior direction to approaching and receding ground optic flow in young, middle-aged and old adults. Our aims were first, to assess postural responses to ground optic flow with respect to the postural task (quiet standing vs. stepping in place) and second, to define motor signatures of increased reliance on the visual reference frame with age.

We hypothesised that changing the somatosensory information provided by the podal contact with the support surface from continuous (quiet standing) to intermittent (stepping in place) would affect the influence of optic flow on body orientation and motion. Old adults and individuals with greater reliance on the visual reference frame, i.e. more visual field dependent, would be more influenced by the visual stimuli while stepping in place. We also considered that approaching and receding flows would differentially affect our participants depending on their profiles, i.e. age and visual field dependence. Young and less visual field dependent individuals would exploit the direction of optic flow and thus appropriately move in the opposite direction. Old and more visual dependent individuals would rather move in the direction of the flow and with greater amplitudes indicating sensitivity to dynamic visual perturbation. Furthermore, if reliance on visual self-motion information with respect to the ground surface increases following a linear trend, middle-aged adults should exhibit a behavioural response between that of young and old adults. Finally, we considered that individuals most reliant on the visual reference frame would be unable to exploit the somatosensory-based egocentric frame of reference.

III.2 Methods

III.2.1 Participants

A total of 56 volunteers participated in the study. They were divided into three age groups: 19 young adults (YA, 10 males, 9 females, age: 31.2 ± 6.3 years), 17 middle-aged adults, (MA, 6 males, 11 females, age: 51.7 ± 5.8 years) and 20 old adults (OA, 10 males, 10 females, age: 74.1 ± 3.7 years). Participants were free

of visual, neurological, musculoskeletal, cardiovascular and vestibular impairments. All reported no past or current symptoms of vertigo or dizziness. They all had a binocular visual acuity of at least 0.10 logMAR with normal or corrected to normal vision. Participants wearing glasses were fully adapted to their lenses. The experimenters verified that differences in visual acuity between the refractive correction worn and optimal correction were under 0.10 logMAR. Visual equipment was kept as usual in daily life during the experimental session. Old adults lived in the community and reported having a fairly active lifestyle. All volunteers were informed of the different test procedures and provided written consent to participate. All tests were performed with the approval of the local ethics committee in accordance with the Declaration of Helsinki.

III.2.2 Experimental set-up

The experiment took place in a 6.7 m x 4.2 m laboratory. A 6 m x 1 m walkway was covered entirely with a white carpet and served as a screen onto which visual stimuli were projected, depending on the experimental condition. A cobblestone pattern was projected onto the walkway covering an area of 4.8 m x 1 m in front of where participants stood. A short throw video projector (Hitachi ED-A101) was mounted on one of the room's side walls in a vertical position in order to project stimuli onto the white carpet. Black curtains were hung over the walls and a plain dark carpet covered the floor in order to provide greater visual immersion and limit any visual elements of reference. When lights were off the laboratory was in the dark except for the illumination from the visual stimulus. Figure III.1a illustrates the experimental set up of our study.

III.2.3 Data acquisition

An 8-camera motion capture system (Bonita B10 Cameras, VICON Motion Systems Inc., Oxford, UK) was used to track and record participants' movements at a sampling frequency of 100 Hz. A force plate (AMTI OR6-5-1000), recording at 500 Hz, was embedded in the walkway and synchronised with the VICON system. The outline of the force plate was drawn onto the white carpet. Participants were equipped with a tight fitting suit on which 37 retro-reflective markers were placed following VICON's Plug-in Gait model. Eight markers were used to obtain head, trunk and foot data: two front and two back markers of the head, two markers of the shoulders and two markers of the posterior superior iliac spine, and two markers on each foot, at the heel and second metatarsophalangeal joint. Centre of pressure data were obtained from the force plate.

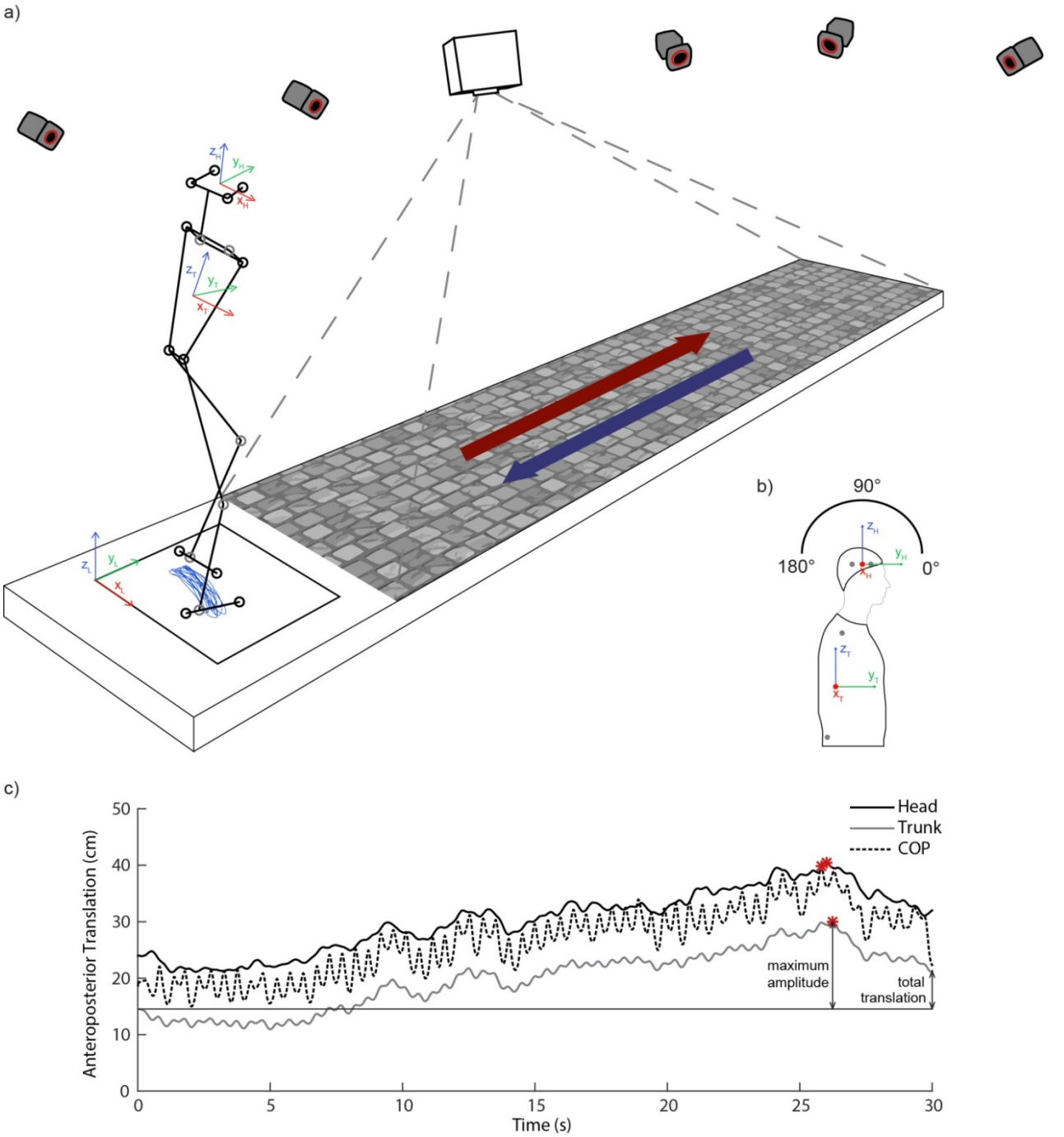

Figure III.1: a) Experimental setup illustrating a participant stepping in place on the force plate, the associated COP trajectory in blue and the cobblestone pattern on the walkway. The visual stimulus moved towards (blue arrow) or away (red arrow) from the participant to create approaching or receding ground optic flow. The retro-reflective markers used for recording the body motion of the participants are represented with black circles. Laboratory, head and trunk coordinate systems are indicated. b) Head and trunk coordinate systems were based on the angular positions calculated during a reference measurement while standing quietly for 10 s. The convention used for pitch angle is illustrated: a position of 90° represents the reference angle measured; values below 90° indicate downward pitch and values above 90° represent backward pitch relative to the reference angle respectively. c) Example of head, trunk and COP translation over the course of one trial for a young participant stepping in place. Asterisks on each curve indicate the point of maximum amplitude for the three body levels.

III.2.4 Visual Stimuli

The cobblestones in the pattern used were spatially irregular, each one measuring about 25 cm x 19 cm and with a texture illustrating an uneven surface. Depending on the experimental condition, the stimuli moved in the anteroposterior (AP) direction relative to the participant in order to create an optic flow in the lower visual field. Considering age-related differences in walking speed, we chose to impose the same visual gain for all our participants by tailoring optic flow speed with respect to the person's preferred walking speed. The optic flow speed was calculated according to the following equation:

$$v_{OF} = v_W * g \quad \text{(III.1)}$$

where v_{OF} is the optic flow speed, v_W is the participants' average preferred walking speed and g is the visual gain.

Participants' preferred walking speed was measured prior to recording of the experimental conditions. They were instructed to walk naturally at a preferred and habitual pace along the 5 m of the walkway. Participants were asked to look straight ahead. Three trials were repeated and walking speed was calculated over the second gait cycle by taking the distance travelled by the sternum marker, over the time taken to travel that distance. Preferred walking speed was estimated as the mean of the three trial measurements (cf. TableIII.1).

Negative or positive visual gain values gave rise to approaching or receding flows respectively. The visual gains used were: -0.5 (approaching flow) and 0.5 (receding flow). For a participant therefore with a preferred walking speed of 1.2 m/s the optic flow speed for each optic flow condition would be -0.6 m/s and 0.6 m/s respectively. We chose a gain of +/- 0.5 since using half the preferred walking speed is commonly used in the literature (e.g. Guerin & Bardy 2008; Mohler et al., 2007).

III.2.5 Procedure

Participants were required to stay on the force plate at the beginning of the walkway for 30s. They were barefoot and instructed to perform one of two tasks: quiet stance (QS) or stepping in place (SIP). Under quiet stance, participants stood naturally on the force plate with a comfortable foot width base and arms hanging by their sides. Participants were instructed to simulate walking without moving forwards or backwards for the stepping in place task. They practised this task prior to recording and were encouraged to adopt a comfortable pace, similar to their habitual walking cadence. For both postural tasks and under every experimental condition, participants were instructed to look straight ahead. Four conditions of visual stimulation were used: natural flow (NF), static stimulation (ST), approaching flow (AF) and receding flow

(RF). Natural flow was our control condition. Recordings in this condition were made with the lights turned on and no projection on the walkway. All other conditions were performed in the dark with only the projection of the cobblestone pattern as a source of light. For the static stimulation condition the cobblestone pattern did not move. For the approaching and receding flow conditions the cobblestone pattern moved towards or away from the participants, respectively.

Natural flow was recorded first, followed by static stimulation, for both postural tasks in order to avoid any visual motion after effect. Optic flow conditions were subsequently recorded. Quiet standing and stepping in place were counterbalanced for each participant to avoid fatigue. The order of the postural tasks and optic flow conditions were randomised between participants. All conditions were performed in blocks of five trials. In total 2 postural tasks x 4 visual stimulation conditions x 5 trials were completed.

The instructions were given before each block of five trials and set breaks were taken every four blocks of trials to avoid fatigue. The total experiment duration averaged an hour and a half.

III.2.6 Data processing

Motion capture and force plate data were filtered with a second order low pass Butterworth filter with a cut off frequency of 3 Hz. Due to the different sampling rates of the motion capture system (100 Hz) and force plate (500 Hz), all signals were resampled to 3000 samples per trial, corresponding to 30 s at a frequency of 100 Hz.

III.2.7 Re-orientation indices

We chose to assess pitch orientation of the head and trunk segments and the kinematics of all three body levels in the sagittal plane in order to examine whether different body-level responses were flow- and/or age-specific. Head and trunk stabilisation are critical in order to provide a stable reference platform for the visual and vestibular systems and maintain stable gaze in adults as well as in children (Assaiante & Amblard, 1993; Pozzo et al., 1990). The centre of pressure (COP) on the other hand is an indicator of the neural control of the ankle muscles (Winter, 1995). Studies examining the effect of optic flow stimuli on postural control have focused their analysis on head (Sparto et al., 2006), trunk (Brady et al., 2012) or COP movements (Borger et al., 1999; Bugnariu & Fung, 2007; Flückiger & Baumberger, 1988; Slaboda et al., 2011; Wade et al., 1995).

Moreover, differential controls of the upper body and lower limbs have been reported (Keshner, Woollacott, & Debu, 1988; Kuno, Kawakita, Kawakami, Miyake, & Watanabe, 1999; Buchanan & Horak, 1999).

Head & Trunk Pitch Orientation

Given that our stimuli were in the sagittal plane, we focused our analysis on pitch rotation. Pitch orientation angles for both head and trunk segments were calculated based on the four head markers, the two shoulder and two posterior superior iliac spine markers. Each segment was considered as a rigid body with its own Cartesian coordinate system, the origin being the centroid of the segment as illustrated in Figure III.1. With the convention we used, an angle of 90° defines the vertical orientation (see Figure III.1b), angles smaller than 90° indicate downward/forwerd pitch and inversely, angles greater than 90° indicate upward/backward pitch. Angular position of the head and trunk were calculated with respect to each participant's own reference orientation. A 90° angle therefore, in any plane signified that the participant's orientation was identical to the one recorded during the reference measurement. Reference orientations were recorded over a period of 10 s while the participant stood quietly looking straight ahead. Lights were on and there was no visual stimulus projected onto the walkway.

Kinematics

We examined anteroposterior translation, given that our ground optic flows moved in that direction to evaluate how the participants' bodies reacted to the different visual stimuli. Measurements were made at three body levels: the centroids of the head and the trunk and the centre of pressure (COP). We calculated four indices tied to body translation: 1- maximum amplitude of translation defined as the greatest deviation, positive (forwards) or negative (backwards), with respect to the participant's initial position, in cm (see Figure III.1c); 2- total body translation from initial to final position, in cm; 3- mean velocity of translation, from the beginning up to the time of maximum translation amplitude, in cm/s; and 4- body-optic flow velocity ratio (BOVR), defined as the mean translation velocity of each body level over the absolute optic flow velocity. Since translation velocity was signed, we took absolute optic flow velocity to maintain the translation sign whereby negative values indicated backwards motion while positive values indicated forwards motion. As translation velocity had units of cm/s and optic flow velocity had units of m/s, the BOVR indicated a percentage of an individual's motor sensitivity to optic flow, calculated for each body level (head, trunk, COP). For the stepping in place task we measured two further kinematic indices: 1- maximum mediolateral COP amplitude in cm and 2- mean stepping frequency, in steps/min. When in single

support stance, the COP is limited to the area of the participant's supporting foot. Mediolateral COP amplitude was therefore an indicator of step width when stepping in place.

III.2.8 Reference frame reliance of our participants

We wanted to examine whether reliance on different reference frames may be associated with the effects of ground optic flow. Reliance on the visual reference frame was assessed via the Rod and Frame Test (RFT) and the Rod and Disc Test (RDT) and reliance on the egocentric reference frame, was assessed via the Rod and Body Test (RBT) for all volunteers in an earlier session (Agathos et al., 2015). Absolute adjustment errors per age group for each test are provided in Table III.1.

Table III.1 : Summary of visual field dependence tests and preferred walking speed for each age group

Age Group	Preferred Walking Speed (m/s)	RFT Absolute Error (°)	RDT Absolute Error (°)	RBT Absolute Error *Tilted-Erect value*[2] (°)
YA	1.34 ± 0.23	2.1 ± 0.8	1.9 ± 0.8	14.5 ± 5.8
MA	1.24 ± 0.17	3.0 ± 1.6	3.3 ± 1.6*	10.9 ±5.5
[2]OA	1.01 ± 0.12*†	7.0 ± 3.8*†	4.9 ± 2.0*†	6.0 ± 4.3*†

*: significant difference with YA
†: significant difference with MA

III.2.9 Statistical Analysis

All indices were averaged across the five trials for each participant to give mean values, while standard deviation across trials revealed intra-individual variability. We subtracted the value obtained under the

[2] The RBT was performed with the body erect and with the body tilted at 70°. When erect, individuals with better egocentric referencing will make hardly any error in estimating the gravitational vertical. When tilted, these individuals will make large errors in the direction of their body tilt (Aubert effect). We took the difference between the error when tilted and when erect as the score for egocentric dependence, larger values indicating better exploitation of the egocentric reference frame (Agathos et al., 2015).

natural flow condition (control) from the other three stimulation conditions for orientation and body translation indices, except the BOVR, in order to obtain relative measures.

Segment angles and body translation indices were subjected to separate analyses of variance (ANOVAs) for the quiet standing and stepping-in-place tasks. All kinematic indices except the BOVR were analysed with an age group (3) x segment/body level (2/3) x visual stimulation (3) repeated measures ANOVA. Mean head and trunk pitch orientations were analysed separately with an age group (3) x visual stimulation (3) repeated measures ANOVA. The BOVR was analysed with an age group (3) x body level (3) x optic flow direction (2) repeated measures ANOVA. The partial eta squared (η^2) was used to determine effect strengths. Tukey's honest significant difference (HSD) test ($p < 0.05$) was used for *post hoc* comparisons. Pearson correlations were performed to examine the relationship between assessments of reference frame reliance (RFT, RDT and RBT) and optic flow sensitivity (BOVR). We examined the sign of the regression slope and R^2 values were used to determine correlation strength, significance being $p < 0.05$.

III.3 Results

III.3.1 Age differences on baseline values

We first examined our participants' behaviour under the control condition to establish any differences that would be due to age. Table III.2 summarises the mean values and standard deviations measured while standing or stepping in place for each age group. Our analysis revealed no age effects for head and trunk pitch orientations. Regarding the kinematic indicators, the old adults showed significantly larger and faster translations at all three body levels (head, trunk and COP) while stepping in place compared to young and middle-aged adults ($p<0.05$) (amplitude: $F(2, 53)=13.09$, $p=0.00$ $\eta^2=0.33$; total translation: $F(2, 53)=15.81$, $p=0.00$, $\eta^2= 0.37$; velocity: $F(2, 53)=10.38$, $p=0.00$, $\eta^2= 0.28$). During quiet stance, a main effect of age group was found only for total translation ($F(2, 53)=4.85$, $p=0.01$, $\eta^2= 0.16$) indicating a greater forward translation of old adults compared to the young ($p<0.05$).

Having thus established baseline values for our population, we proceed to describe results of our analyses on the relative values under visual stimulation conditions. We normalised all indicators, i.e. pitch orientation and kinematic behaviour, during static stimulation, approaching and receding flow with respect to participant data during the control condition except for the BOVR. This was done to ensure a deeper understanding of ground optic flow sensitivity.

Table III.2 : Summary of variable values under the control condition for both tasks and all three age groups

Task:		**QS**			**SIP**		
Age group:		***YA***	***MA***	***OA***	***YA***	***MA***	***OA***
Mean Pitch Orientation (°)	Head	89.75 ± 0.64	89.96 ± 0.59	89.97 ± 0.48	90.31 ± 3.67	93.54 ± 3.14	90.67 ± 5.32
	Trunk	89.97 ± 0.09	90.16 ± 0.67	89.96 ± 0.12	86.56 ± 2.45	86.70 ± 1.88	86.09 ± 2.47
Maximum Translation Amplitude (cm)	Head	-0,55 ± 1,35	0.00 ± 2.08	1.01 ± 2.31	8.98 ± 8.19	9.00 ± 8.51	**21.08 ± 9.11 *†**
	Trunk	0.98 ± 0.87	-0.56 ± 1.64	-0.20 ± 1.51	7.08 ± 7.76	8.56 ± 9.01	**20.58 ± 8.49 *†**
	COP	1.25 ± 1.05	1.75 ± 1.04	1.84 ± 2.02	10.07 ± 8.82	12.53 ± 9.49	**22.65 ± 9.05 *†**
Total Translation (cm)	Head	0.30 ± 0.94	0.07 ± 1.19	**0.72 ± 1.53 ***	8.10 ± 6.37	8.23 ± 7.59	**19.32 ± 9.21*†**
	Trunk	-0.71 ± 0.65	-0.34 ± 0.82	**0.23 ± 1.02 ***	6.62 ± 5.95	7.25 ± 7.53	**18.45 ± 9.12 *†**
	COP	0.33 ± 0.69	0.69 ± 0.71	**0.93 ± 1.12 ***	3.87 ± 5.72	4.30 ± 7.99	**17.13 ± 9.03 *†**
Translation Velocity (cm/s)	Head	-0.26 ± 0.39	-0.05 ± 0.72	-0.02 ± 0.68	1.81 ± 1.84	2.10 ± 2.40	**4.65 ± 2.08 *†**
	Trunk	-0.30 ± 0.27	-0.13 ± 0.59	-0.09 ± 0.47	1.17 ± 1.86	2.09 ± 2.65	**4.58 ± 2.04 *†**
	COP	0.23 ± 0.24	0.47 ± 0.53	0.23 ± 0.57	2.18 ± 2.37	2.98 ± 2.87	**5.13 ± 2.36 *†**
Mean stepping frequency (steps/min)					103 ± 10	108 ± 20	100 ± 17
Maximum mediolateral COP amplitude (cm)					22.95 ± 3.01	25.14 ± 4.42	26.04 ± 4.77

*: significant difference with YA
†: significant difference with MA

III.3.2 Angular versus kinematic indicators

We examined the head and trunk re-orientation behaviour in pitch during stepping in place and quiet standing, results are presented in Figures III.2 and III.3. We identified a mean head pitch re-orientation

induced by the dynamic visual stimuli relative to static stimulation under both stepping in place ($F(2, 106)=7.75$, $p=0.001$, $\eta^2=0.13$) and quiet standing ($F(2, 106)= 25.79$, $p=0.000$, $\eta^2=0.33$) as revealed by main effects of visual stimulation. Tukey's HSD revealed that the head tilted backward in the presence of moving ground optic flow for both directions compared to static stimulation ($p<0.05$). Approaching and receding optic flow effects on head pitch orientation did not differ significantly. The mean head pitch angles observed relative to the control condition were 0.49° under static stimulation and 2.73° under the optic flow conditions (average of approaching and receding flow) during quiet standing and were 0.22° and 1.75°, respectively while stepping in place. There was a difference between optic flow directions on mean trunk pitch orientation however. During quiet stance a main effect of visual stimulation ($F(2, 106)=11.00$, $p=0.000$, $\eta^2=0.17$) revealed that the trunk was held further back under approaching flow compared to static stimulation and receding flow ($p<0.05$). During stepping in place there was a similar trend ($p=0.056$). No age effects were found, indicating that re-orientation of the head and trunk in pitch were similar across all three age groups.

We next examined the maximum translation amplitude, total translation and mean velocity of translation for both postural tasks, as well as mean stepping frequency and maximum mediolateral COP amplitude, i.e. step width, for stepping in place. We actually found that the visual stimulation effect for mean stepping frequency ($F(2, 106)=11.89$, $p=0.000$, $\eta^2= 0.18$) and step width ($F(2, 106)=4.19$, $p=0.02$, $\eta^2= 0 .07$) was similar to that of head pitch orientation, i.e. not optic flow direction-specific. Tukey's HSD revealed a higher stepping frequency and larger step width under both optic flow direction conditions compared to static stimulation ($p<0.05$). In addition, old adults had a greater stepping frequency than the young ($F(2, 53)=3.24$, $p=0.047$, $\eta^2= 0.11$). Step width and frequency values for our three age groups under visual stimulation conditions are indicated in Table III.3.

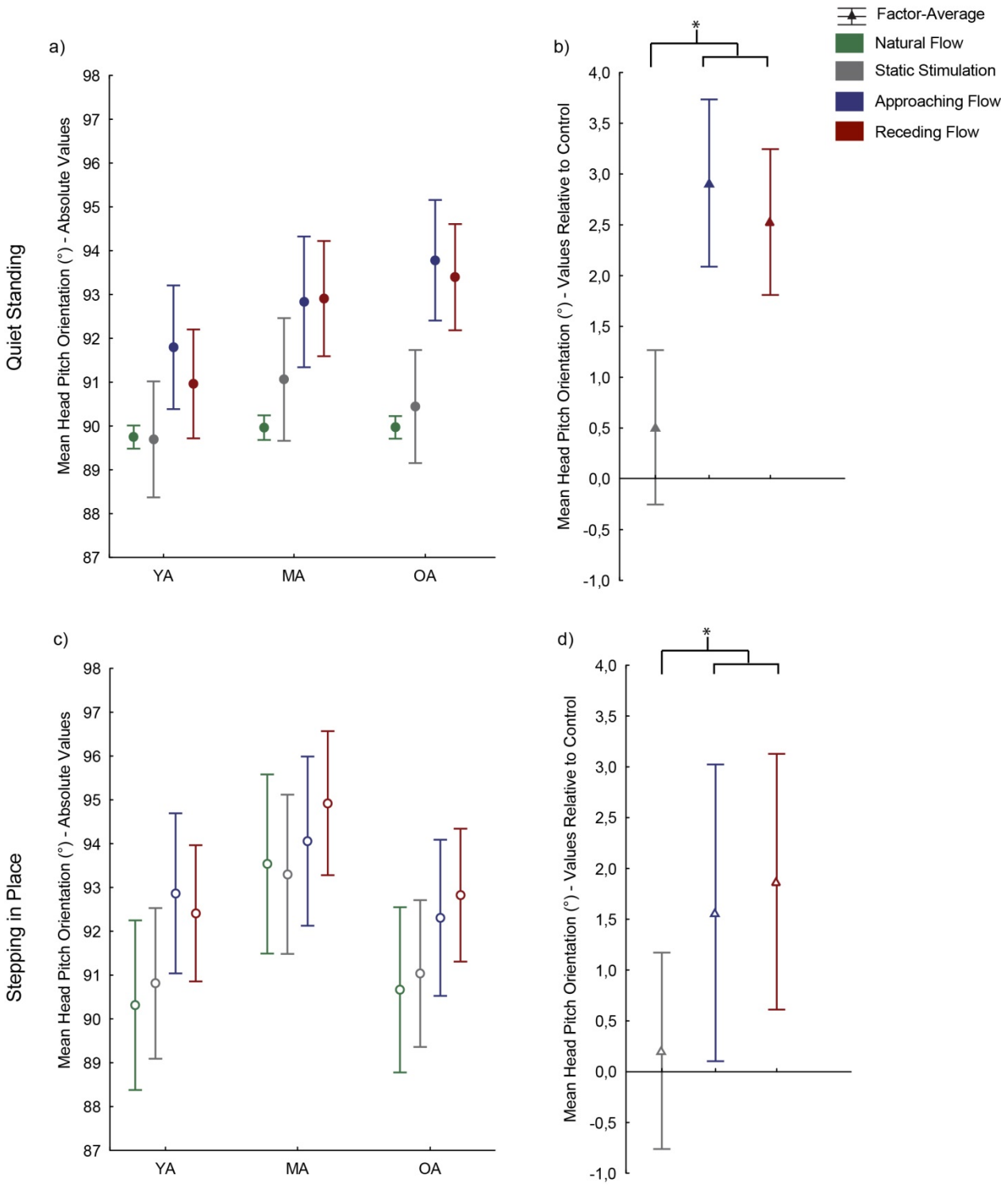

Figure III.2 Mean head pitch orientation during quiet stance (top) and stepping in place (bottom). Absolute values of mean head pitch orientation during quiet stance (a) and stepping in place (c) under each visual stimulation condition. Mean values, averaged across participants relative to the control condition reveal main effects of visual stimulation during standing (b) and stepping in place (d). Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults

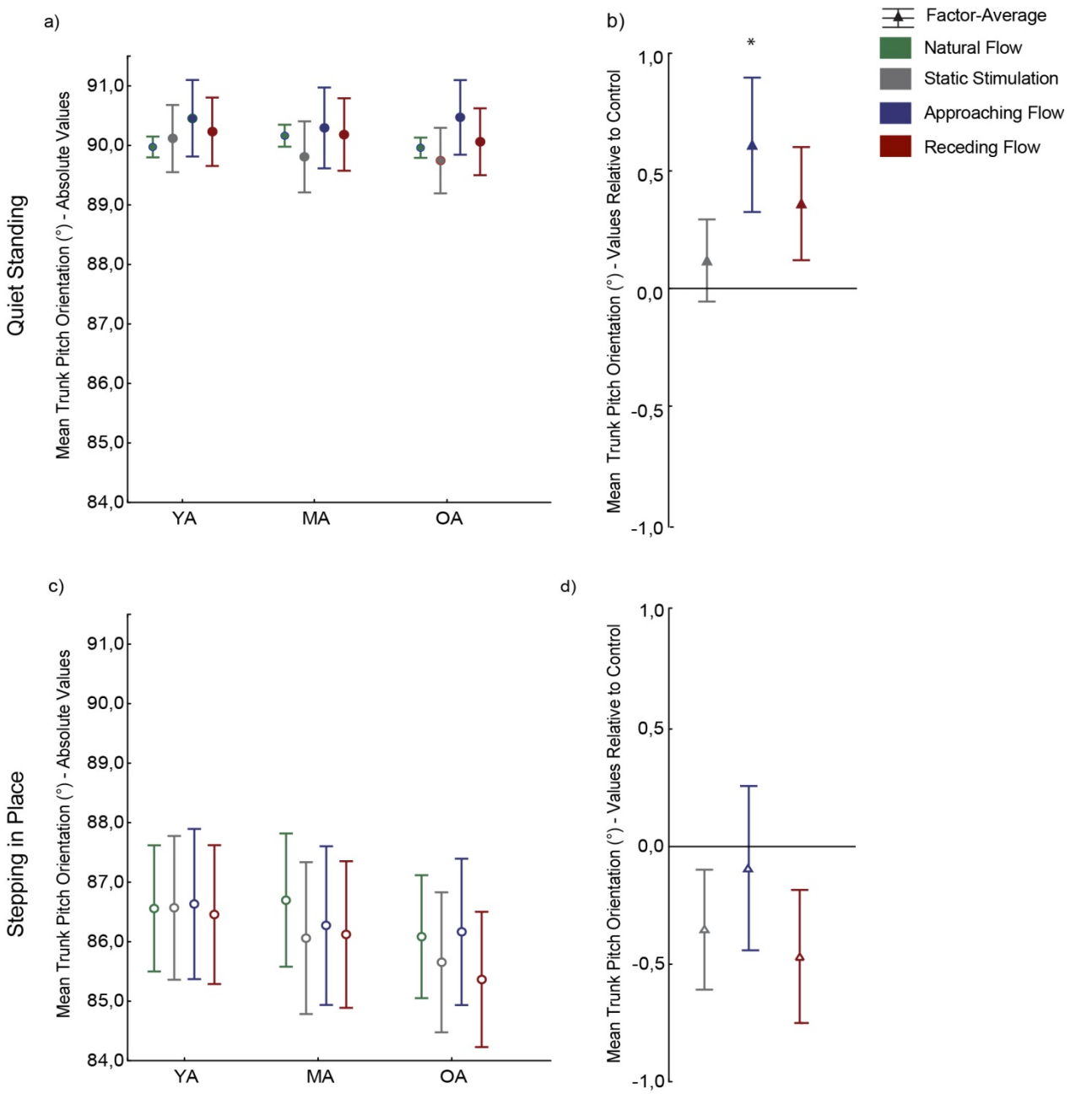

Figure III.3 Mean trunk pitch orientation during quiet stance (top) and stepping in place (bottom). Absolute values of mean trunk pitch orientation during quiet stance (a) and stepping in place (c) under each visual stimulation condition. Mean values, averaged across participants relative to the control condition reveal main effects of visual stimulation during standing (b) and stepping in place (d). Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults

A directional effect (approaching versus receding optic flow) was found however for maximum amplitude ($F(2, 106)=13.13$, $p=0.00$, $\eta^2= 0.20$), total translation ($F(2, 106)=16.27$, $p=0.00$, $\eta^2= 0.24$) and mean velocity ($F(2, 106)=7.55$, $p=0.00$, $\eta^2= 0.12$) during stepping in place. Participants drifted when faced with ground optic flow. The ANOVA revealed significant differences for all three translation indicators between approaching flow and the other two visual stimulation conditions ($p<0.05$). The analysis revealed a backward

and slower translation under approaching flow compared to static stimulation and receding flow. Interestingly, the visual stimulation effect was different during quiet standing and only observed for total translation ($F(2, 106)=6.06$, $p=0.00$, $\eta^2= 0.10$), as may be seen in Figure III.4. During quiet standing, approaching flow did not lead to a backward translation compared to static stimulation as during stepping in place. Rather, we observed a forward translation on average for the receding optic flow compared to static stimulation and approaching flow ($p<0.05$). Kinematics results were independent of body level and of age except for the total translation in both tasks and for the stepping frequency during stepping in place. For total translation, we noticed a simple age effect during quiet standing ($F(2, 53)=4.27$, $p=0.02$, $\eta^2= 0.14$) and an age vs. visual stimulation interaction effect during stepping in place ($F(4, 106)=2.88$, $p=0.03$, $\eta^2= 0.10$). During quiet standing, old adults differed significantly from young adults ($p<0.05$) with a total translation further back than the control condition. During stepping in place, the interaction effect revealed that young adults did not show directional behaviour with respect to optic flow or an effect of static versus dynamic stimulation contrary to middle-aged and old adults ($p<0.05$) as may be seen in Figure III.4. For middle-aged and old adults, total translation was further back under approaching flow compared to static stimulation and receding optic flow conditions ($p<0.05$) revealing a modulation under the more ecological optic flow condition. In addition, a simple effect of age ($F(2, 53)=3.24$, $p=0.047$, $\eta^2= 0.11$) was found for stepping frequency revealing that old adults had a higher stepping frequency on average compared to young adults ($p<0.05$).

Table III.3 : Stepping frequency and step width. Values relative to control under each imposed visual stimulation condition for each age group. Means indicated with standard deviation.

	Mean Stepping Frequency Relative to Control (steps/min)			**Maximum mediolateral COP Amplitude (Step Width) Relative to Control (cm)**		
Visual Stimulation Condition	**YA**	**MA**	**OA**	**YA**	**MA**	**OA**
Static Stimulation	1,87 ± 5,18	3,53 ± 5,68	5,62 ± 5,72	0,04 ± 1,21	0,49 ± 1,40	0,97 ± 1,36
Approaching Flow	2,18 ± 6,48	7,23 ± 10,75	8,74 ± 7,66	0,70 ± 2,40	1,23 ± 2,36	1,64 ± 2,31
Receding Flow	3,92 ± 6,05	6,03 ± 11,60	10,68 ± 7,09	0,72 ± 1,71	0,92 ± 2,89	2,00 ± 2,24

*: significant difference with YA
†: significant difference with MA

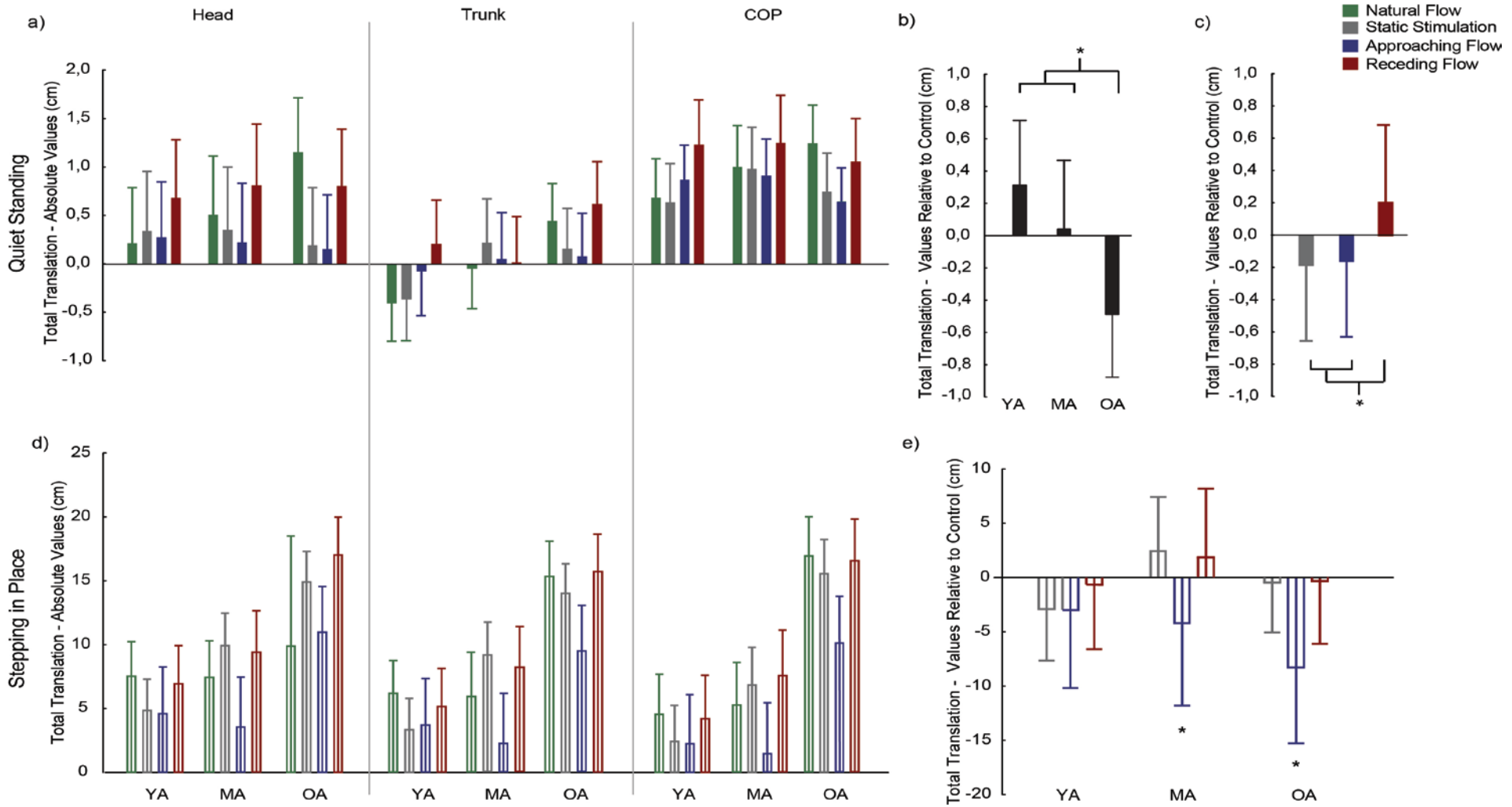

Figure III.4: Total translation during quiet standing (top) and stepping in place (bottom). Absolute values of the head (left), trunk (centre) and COP (right) under each visual stimulation condition are presented during quiet standing **(a)** and stepping in place **(d).** Values averaged across body levels and relative to the control condition are presented to indicate the main effects of age **(b)** and visual stimulation **(c)** during quiet stance and the age group vs. visual stimulation interaction effect **(e)** during stepping in place. Bar heights indicate mean values with error bars representing 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults.

III.3.3 Optic flow direction sensitivity

Unlike the above indices, the body-optic flow velocity ratio data analysed were not relative to the control condition. The BOVR represents a ratio of participant translation velocity over the absolute velocity of the optic flow projected on the ground. Therefore there exists no baseline value, simply because there was no optic flow projected during the control condition. Optic flow velocity, however, is based on participants' preferred walking speed. The BOVR therefore does contain a self-referencing aspect which takes aging into account given that there exists a significant age difference in preferred walking speed (cf. Table III.1). In addition, as translation velocity and maximum amplitude under all optic flow conditions were very highly correlated (R^2 = 0.7 to 0.9), we can be assured that larger velocities were associated with greater translations, either forwards (positive values) or backwards (negative values).

For the quiet standing task, we found only an effect of body level ($F(2,106)=36.03$, $p=0.00$, $\eta^2= 0.40$) indicating a greater influence of optic flow on the centre of pressure compared to the head and the trunk ($p<0.05$). This body level effect was also observed during stepping in place ($F(2,106)=18.58$, $p=0.00$, $\eta^2=0.26$). In addition our analysis showed a significant body level vs. optic flow direction interaction effect ($F(2, 106)=35.38$, $p=0.00$, $\eta^2=0.40$) when stepping in place. Tukey's HSD revealed that the COP was more influenced than the head and trunk under both optic flow directions ($p<0.05$), revealing a backward drift for approaching flow (-4.06 ± 5.66 %) and a forward drift for receding flow (6.59 ± 6.04%). In addition, results revealed a significant age effect ($F(4,106)=6.11$, $p=0.00$, $\eta^2=0.44$) whereby old adults were more sensitive to optic flow stimulation than the young and middle-aged ($p<0.05$). In agreement with the greater translation amplitude revealed in the control condition, this result confirms that old adults have a weaker control of body position in space. Indeed, at the centre of pressure level, the percentage of effect in the old adult group was on average -7.67% under approaching flow and 11.82 % under receding flow. A significant interaction effect between age and optic flow direction ($F(2, 53)=14.97$, $p=0.00$, $\eta^2=0.36$) revealed that middle-aged and old adults had significantly larger absolute BOVR values in receding compared to approaching flow (values being positive for receding and negative for approaching flow). Interestingly, only under the less ecologic, receding flow did the old have significantly larger BOVR values than the young and middle-aged adults ($p<0.05$). The age group vs. body level vs. optic flow direction interaction effect ($F(4, 106)=7.98$, $p=0.00$, $\eta^2=0.23$), as seen in Figure III.5, further revealed that the greater optic flow direction influence on the COP appeared for all three age groups and that old adults showed greater sensitivity at the level of the COP under both optic flow conditions compared to the other two age groups ($p<0.05$).

Finally, we examined the intra-individual variability of the BOVR to assess the robustness of the behaviour observed. If the velocity ratio is indeed a good indicator of optic flow sensitivity, the visual stimulus should not influence intra-individual variability. Our analysis revealed a significant main effect of age during both quiet standing ($F(2, 53)=10.68$, $p=0.00$, $\eta^2=0.29$) and stepping in place ($F(2, 53)=3.68$, $p=0.03$, $\eta^2=0.12$). It appears that old adults were significantly more variable than the young and middle aged when standing

(p<0.05), though this difference existed only between the old and the young when stepping in place (p<0.05). The variability was also different depending on the body level. Under quiet stance a simple body level effect ($F(2, 106)=10.56$, $p=0.00$, $\eta^2=0.17$) revealed greater variability at the head level compared to the trunk and COP (p<0.05), while a body level vs. age interaction ($F(4, 106)=2.93$, $p=0.02$, $\eta^2=0.10$) under stepping in place showed that old adults had significantly greater head variability compared to young adults (p<0.05). No effect of optic flow direction was observed however. To summarise, directional sensitivity to optic flow was best revealed by the COP-optic flow velocity ratio (COVR) during stepping in place and this variable is a robust index given that it was not influenced by the direction of optic flow.

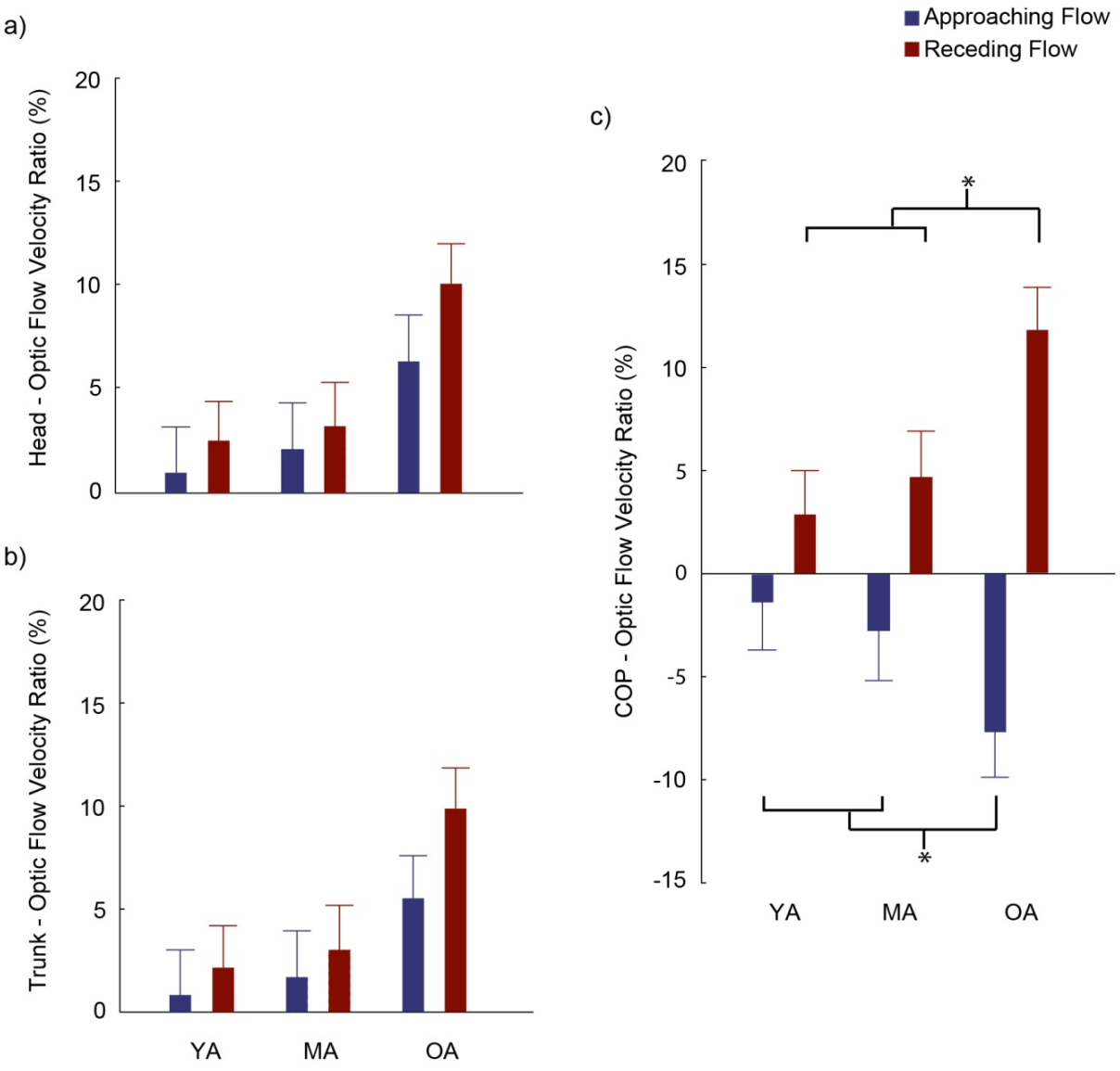

Figure III.5: Body-optic flow velocity ratio at the level of (a) the head, (b) the trunk and (c) the COP under approaching and receding optic flows. Positive and negative values indicate forward and backward motion respectively. Bar heights indicate mean values with error bars representing 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults.

III.3.4 Aging and ground optic flow sensitivity

In order to better understand the effect of aging under dynamic visual stimulation, we performed a segmentation analysis on the COP-optic flow velocity ratio to identify whether inter-individual differences exist regarding the sensitivity to approaching and receding ground optic flow. A k-means clustering analysis was parameterised in order to separate participants into two classes per age group, maximizing inter-class distances and minimizing intra-class variability. As illustrated in Figure III.6, our results revealed a significant segmentation for all age groups under approaching flow and for the young and old adults under receding flow ($p<0.05$). In each age group, we have one class showing a directional sensitivity to optic flow (approaching versus receding), moving on average backwards under approaching and forwards under receding flow. In the second class, the average velocity ratio values are smaller in magnitude, but the directional sensitivity is not identical across the three age groups.

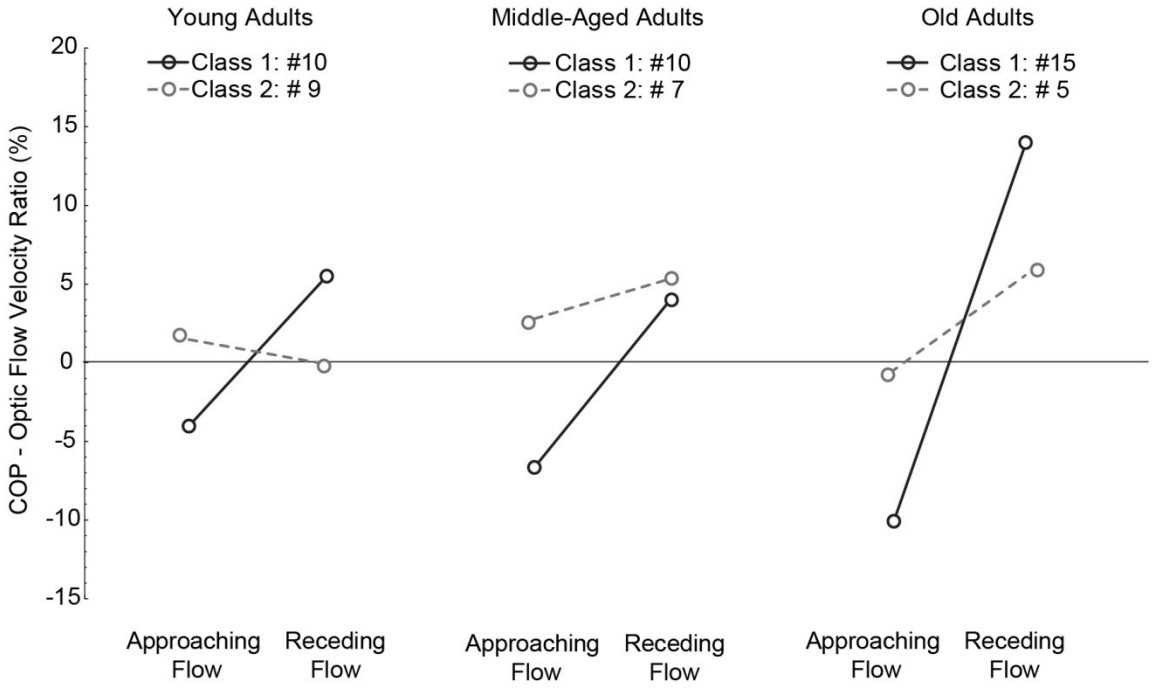

Figure III.6: Optic Flow Sensitivity Segmentation. Segmentation per age group was based on the COP-optic flow velocity ratio under each optic flow direction. Number of participants is indicated for each class in each age group.

As we see in figure III.6, with increasing age group, the magnitude of the velocity ratio values increases for the 1st class (directionally sensitive to optic flow): negative for approaching flow and positive for receding

flow. Sensitivity vs. optic flow direction interaction effects were observed for all three age groups (YA: F(1, 17)=82.50, p=0.00, η^2= 0.83; MA: F(1, 15)=7.74, p=0.01, η^2=0.34; OA: F(1, 18)=56.28, p=0.00, η^2=0.76). Globally, we may characterise participants in the 1st class as being more directionally sensitive to optic flow, as revealed by significant differences between optic flow direction conditions in this class via Tukey's HSD ($p<0.05$). The individuals of the 2nd class among young adults actually moved forwards under both optic flow direction conditions. With the smallest differences from zero, these participants showed the least sensitivity to optic flow as well as no directional sensitivity. In the middle-aged group, the 2nd class differed from the 1st class only under approaching flow. Middle-aged adults of the 2nd class moved forwards, like the young under both optic flow direction conditions, though their velocity ratio values were greater than those of the young. Finally, for the 2nd class of old adults, approaching flow had little effect on COP motion while there was still a tendency to be pulled forwards by receding flow. For this age group, a significant difference existed between approaching and receding flow in individuals of the 2nd class ($p<0.05$).

III.3.5 Optic flow sensitivity and reference frame reliance

We wanted to explore whether and how reliance on visual and egocentric frames of reference were related to optic flow sensitivity. Since the aforementioned sensitivity classes were characterised by the magnitude of the COP-optic flow velocity ratio under each optic flow direction condition, we examined reference frame reliance with respect to the sum of absolute COVR values for approaching and receding flow. Results showed that optic flow sensitivity was indeed linked to reference frame reliance as seen in Figure III.7. The correlation was positive for the RFT ($R^2 = 0.37$, $p = 0.00$) and RDT ($R^2 = 0.26$, $p = 0.00$) and negative for the RBT ($R^2 = 0.27$, $p = 0.00$). We also considered whether the extent of egocentric self-motion perception could be linked to the larger COVR observed under dynamic visual stimulation. We therefore performed a correlation analysis between the absolute maximum translation amplitude of the COP under natural flow (control condition) and the sum of absolute COVR values for approaching and receding flow. As illustrated in Figure III.8, greater optic flow sensitivity was positively correlated to stepping drift when there was no stimulus, i.e. natural drift ($R^2 = 0.47$, $p = 0.000$). This relationship revealed that individuals who drifted when instructed to step in place without any visual stimulus were more carried away by a moving visual stimulus. Visual sensitivity as established by the COVR may therefore be tied to diminished egocentric self-motion perception.

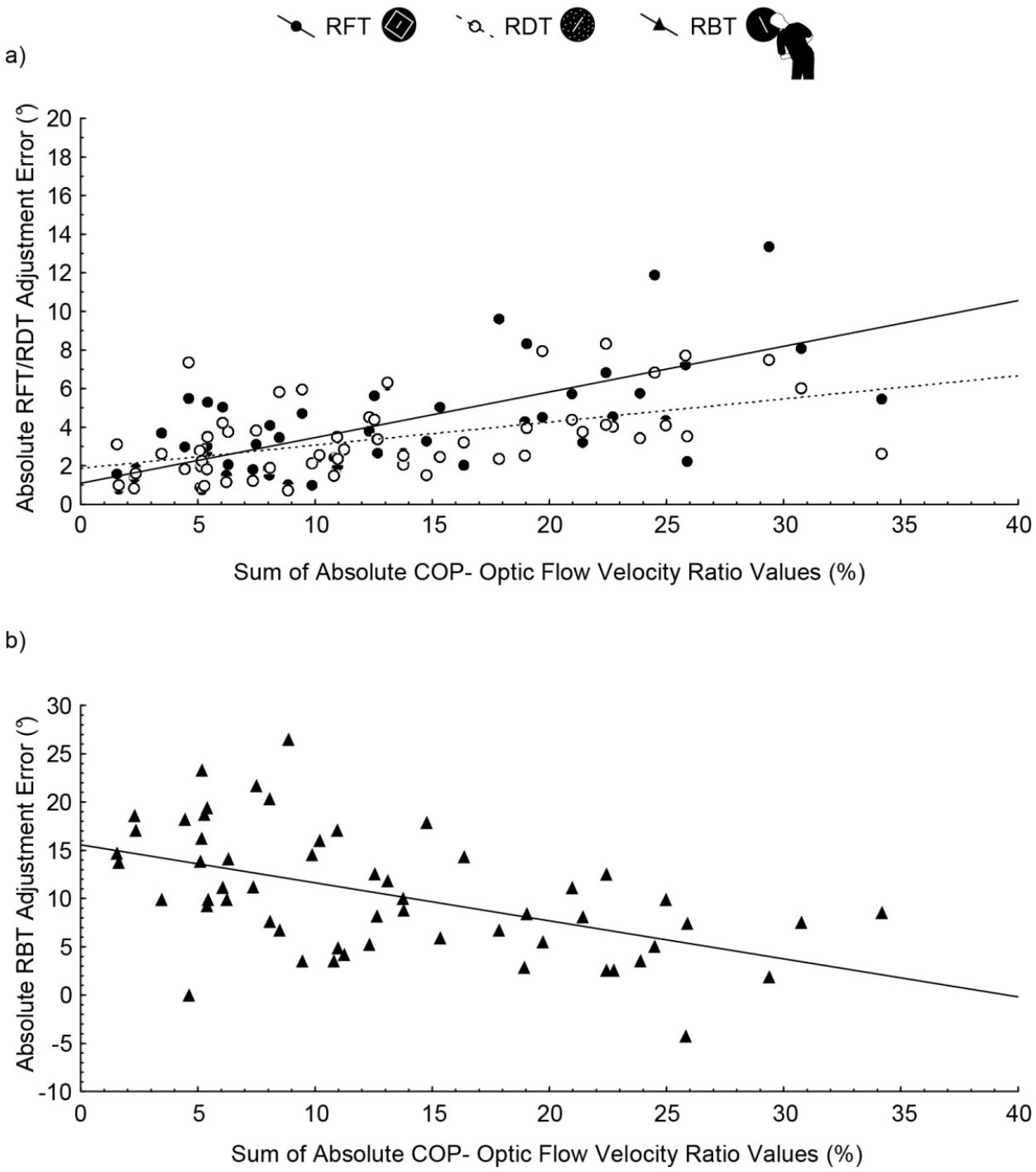

Figure III.7: Relationship of optic flow sensitivity with reference frame reliance. Sensitivity is expressed as the sum of absolute COVR values under optic flow conditions and plotted against visual (a) and egocentric (b) reference frame reliance, assessed by the RFT/RDT and RBT respectively.

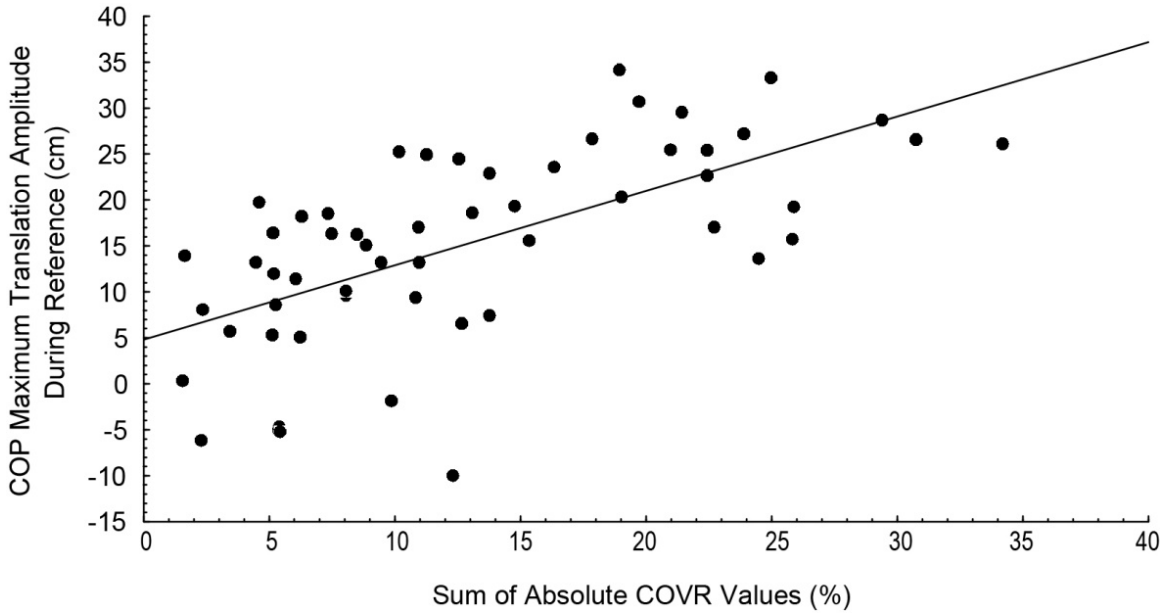

Figure III.8 : Relationship of optic flow sensitivity with egocentric self-motion perception. The former is expressed as the sum of absolute COVR values under optic flow conditions and the latter is expressed as the absolute maximum translation amplitude during the natural flow (control) condition (natural drift).

III.4 Discussion

This study examined firstly how the effects of approaching and receding optic flow projected on the ground may influence self-motion and self-orientation during a permanent or intermittent podal contact with the ground support surface. Secondly this study investigated how such effects may be modulated by age and perceptual reliance on the visual and somatosensory-based egocentric frame of reference. Our experiment revealed six main results:

i. no directional effects of ground optic flow on head pitch orientation, or on stepping parameters, i.e. step frequency and step width,
ii. ground optic flow effects depended on the podal contact and were maximized by stepping in place,
iii. ground optic flow sensitivity increased with age, as revealed by greater amplitudes of the COP-optic flow velocity ratio in both directions,
iv. increased ground optic flow sensitivity with age was linked to an enhanced reliance on the visual reference frame, reduced reliance on the egocentric frame of reference
v. and to poor egocentric self-motion perception, as expressed by COP drift while stepping in place under natural flow (the control condition)
vi. middle-aged adults in addition to old adults showed reliance on visual rather than egocentric self-motion information with respect to the ground surface.

III.4.1 Multisensory integration and self-motion perception: drifting while stepping in place

Integration of multisensory information is crucial for postural control. Models of postural control (Oie et al., 2002; Peterka & Loughlin, 2004) have proposed that controlling both self-motion and self-orientation depends on how the central nervous system dynamically combines and reweights the kinematic and kinetic cues of body-task-environment interactions. The relative weight accorded to different sensory information may therefore be evaluated by introducing conflicting cues to self-orientation and self-motion. Moreover, multisensory integration and reweighting for postural control is particularly sensitive to age as old adults have greater difficulty not only in adapting when sensory information is reduced or discordant but also in taking advantage of sensory redundancy (Hay et al., 1996) and sensory re-integration following perturbation (Doumas & Krampe, 2010; Teasdale, Stelmach, Breunig, & Meeuwsen, 1991). Contrary to previous studies evaluating postural reactions to discordant visual and somatosensory information, we did not perturb the size (Streepey et al., 2007), inclination (Slaboda & Keshner, 2012; Wang, Kenyon, & Keshner, 2010), dynamic stability (Keshner, Kenyon, & Langston, 2004; Mergner, Schweigart, Maurer, & Blümle, 2005) or firmness (Teasdale et al., 1991a; Nougier, Bard, Fleury, & Teasdale, 1997) of the support surface. Rather, by introducing the task of stepping in place, we interrupted the constancy of participants' somatosensory-based body-on-support perception provided by the podokinetic system (Weber et al., 1998). Indeed, were it not for the loss of the constancy of the surface support while stepping in place, drifting would not have been possible.

Drifting while stepping in place was observed under natural flow where no visual stimulus was projected onto the ground, and to a greater extent among old adults (see Table III.2). The fact that this drift occurred even without conflicting visual information indicates a reduction in egocentric self-motion perception with age. This could result from age-related degradation in either or both vestibular and somatosensory information integration. Indeed, a measure of drift while stepping in place is commonly used to screen for vestibular dysfunction. The Fukuda stepping test (Fukuda, 1959) requires participants to step in place with eyes closed and the drift that occurs is measured in terms of amplitude and rotation. Although frailer old adults have trouble completing the test (Lord, Sherrington, & Menz, 2005) and in healthy old adults, it may be used as a gross evaluation of vestibular function, the test's sensitivity and reliability have been criticised (Bonanni & Newton, 1998; Honaker, Boismier, Shepard, & Shepard, 2009; Lord, Menz, & Tiedemann, 2003). Moreover the indication of vestibular deficit lies in the angular deviation of the stepping drift. We did not evaluate angular deviation while stepping in place; however, the linear head acceleration of our participants ranged from 0.005 to 0.011 m/s² (95% confidence interval), which is below the vestibular detection threshold reported in the literature (Benson, Spencer, & Stott, 1986; Israel & Berthoz, 1989;

Kingma, 2005). We therefore consider that the natural drift observed in old adults is due to age-related deficits in somatosensory integration leading to diminished somatosensory-based body-on-support coding. Reductions in somatosensation with age, including proprioceptive acuity, have been previously demonstrated (Boisgontier, Olivier, Chenu, & Nougier, 2012; Shaffer & Harrison, 2007). Supporting our reduced somatosensory-based self-motion perception hypothesis in old adults are also studies reporting a reduced ability to detect and limit body sway due to proprioceptive deficits (Sparto et al., 2006) and the association found between reduced sensation in the lower limbs and dynamic balance tested during a stepping in place task in old adults (Lord, Clark, & Webster, 1991c). In addition, somatosensory information processing is cognitively demanding given that cues stem from multiple sources (e.g. mechanoreceptors at the muscles and joints, pressure sensors at the soles of the feet etc.) and the need to account for multiple degrees of freedom in motor actions. It makes sense therefore that such sensory information processing is compromised in older adults given that a general slowing in information processing (Salthouse, 2000), non-specific recruitment and over-activation of brain regions (Heuninckx, Wenderoth, & Swinnen, 2008; Ward, Swayne, & Newton, 2008; Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005), as well as an increase in interhemispheric transit times (Jeeves & Moes, 1996) occur with age.

In agreement with previous studies (Baumberger, Isableu, & Flückiger, 2004; Dokka, Kenyon, Keshner, & Kording, 2010; Flückiger & Baumberger, 1988; Keshner & Kenyon, 2000; Slaboda, Barton, Maitin, & Keshner, 2009; Sundermier et al., 1996) we found that optic flow influenced our participants' postural kinematics. Our finding of greater optic flow influence in old adults for all the kinematic variables studied also support the widely accepted understanding that visual information is upweighted in old age (Borger et al., 1999; Sundermier et al., 1996; Wade et al., 1995). Under approaching flow, middle-aged and old adults moved backwards, as demonstrated by their drift (maximal and total translation as well as mean translation velocity) while stepping in place (see Figure III.4 for total translation). We assume this is an indication of a greater sensation of forwards self-motion and these participants reacted by countering this perception. We consider that young adults did not differ significantly in their behaviour between the visual stimulation conditions due to their better ability to reweight and disambiguate conflicting sensory information (Oie et al., 2002). An alternative hypothesis for the middle-aged and old adults' backward drift under approaching flow could be that it is an indication of recalibration with respect to the visual stimulus in order to reduce visual-somatosensory conflict in self-motion information. Indeed, studies have revealed proprioceptive adaptation in arm movements under visual conflict (Bernier, Chua, & Franks, 2005), as well as in stepping (Weber et al., 1998) and jogging (Anstis, 1995) under podokinetic stimulation. However, given that we observed natural drift in our control condition where no visual stimulus was projected on the ground, we maintain that drifting while stepping in place indicates a poor egocentric perception of one's self-motion. Participants showing greater drift under conditions of optic flow favour visual over somatosensory body-on-support coding for self-motion perception. Moreover our results indicate that poor self-motion perception is positively correlated with sensitivity to optic flow (expressed by the COVR). We have therefore demonstrated a link between reliance on visual and neglect of somatosensory information for self-motion

perception. This is in agreement with studies reporting upweighting of visual input when somatosensory information is compromised by task constraints in young adults (Isableu & Vuillerme, 2006; Lee & Lishman, 1975; Mergner, Schweigart, Maurer, & Blümle, 2005; Streepey et al., 2007) as well as by age (Judge, King, Whipple, & Clive, 1995; Manchester, Woollacott, Zederbauer-Hylton, & Marin, 1989).

III.4.2 Reference frame reliance – association with age and optic flow sensitivity

How sensory information is weighted can depend on one's reliance on a particular frame of reference as well as the task and environmental demands (Bernardin, Isableu, Fourcade, & Bardy, 2005; Gueguen, Vuillerme, & Isableu, 2012; Isableu et al., 2010). We selected the task of stepping in place in addition to quiet standing as a means to potentially affect somatosensory body-on-support coding (Mergner & Rosemeier, 1998). We enquired as to how the egocentric reference frame is exploited for self-motion perception due to the intermittent podal contact with the ground surface which bears special ecological significance as a reference. The influence of the visual stimuli during quiet standing may have been attenuated given that the permanent podal contact with the ground facilitates somatosensory body-on-support perception. Indeed, proprioception, from the lower limbs in particular, in terms of sensory feedback is crucial for maintaining balance during upright stance (Fitzpatrick & McCloskey, 1994; Fitzpatrick, Rogers, & McCloskey, 1994). While stepping in place, on the other hand, it is the somatosensory body-on-support perception that is attenuated and therefore considered less reliable, thus enhancing the influence of visual information, which is considered more reliable, in coding body orientation relative to visual space.

We hypothesised that stepping in place would allow us to observe a differential influence of optic flow between age groups. Given that reliance on the visual reference frame increases with age (Agathos et al., 2015; Eikema, Hatzitaki, Tzovaras, & Papaxanthis, 2012; Kobayashi et al., 2002; Marendaz, 1984; Panek, Barrett, Sterns, & Alexander, 1978; Schwatz & Karp, 1967; Slaboda et al., 2011) we expected old adults to be more influenced by the ground optic flow than the younger participants. Analysis of the body-optic flow velocity ratio revealed a finer influence of optic flow on the participants' motion while stepping in place. We consider that the BOVR reveals how the visual stimulus is transcribed in the motor behaviour rather than the effect of optic flow on an individual stepping in place, i.e. translation. Inherently, this result also reveals the degree to which visual as opposed to somatosensory information is used to relate self-motion with respect to the ground surface, and particularly at the level of the COP. Therefore, we may consider the COP-optic flow velocity ratio as a motor index of reliance on the visual reference frame for self-motion perception and refer to this index as the *visual self-motion quotient*.

As expected, old adults showed greater sensitivity to ground optic flow as shown by the BOVR values. This is also evidenced by the cluster analysis of the COVR per age group while stepping in place: optic flow

sensitivity increased with age and the composition of the first, more sensitive class comprised a larger proportion of the individuals in the old adult age group. Moreover, the different optic flow direction effects highlight the increase in reliance on the visual reference frame with age. Receding flow differentiated old adults from the middle-aged and the young. Under approaching flow, on the other hand, the difference lied only between the young and the old. This shows that the less frequent receding flow impacted old adults to a greater degree than the other two age groups, while under the more ecological, approaching flow condition, middle-aged adults were no longer significantly different from either of the two other groups. This may be an early indication of middle-aged adults' evolution towards a diminished ability to disambiguate egocentric from visual self-motion perception. We hypothesise that this is not an issue under receding flow given that the visual cue to self-motion is less credible than under approaching flow.

In addition, significant positive correlations were found between increased optic flow sensitivity and increased reliance on the visual reference frame as assessed by the Rod and Frame Test and the Rod and Disc Test. However, the increased reliance on the visual reference frame with age may be a result of a diminished ability to exploit the egocentric reference frame (somatosensory body-on-support coding). Indeed, in young adults placed in challenging situations, individuals with greater reliance on the visual reference frame demonstrated difficulties in exploiting the more reliable somatosensory cues (Brady et al., 2012; Isableu et al., 2010). Similar reports have been made for Parkinsonian patients (Vaugoyeau, Viel, Assaiante, Amblard, & Azulay, 2007) and adolescents (Viel et al., 2009). Moreover, in the tasks assessing reliance on each respective reference frame for spatial orientation in our population, an inverse relationship had been found between visual and egocentric referencing (Agathos et al., 2015). In the present paper a significant correlation was found between greater optic flow sensitivity and reduced reliance on the egocentric reference frame in terms of spatial orientation as assessed with the Rod and Body Test. In addition, we found an even stronger positive correlation between natural drift and optic flow sensitivity. In our previous study, we evoked the fact that the egocentric reference, as evaluated by the Rod and Body Test is diminished with age (Agathos et al., 2015). We argued that the diminished Aubert effect observed in old adults revealed a less salient somatosensory-based idiotropic vector (Mittelstaedt, 1983), and hence these participants have more trouble exploiting the somatosensory cues related to axes of the egocentric reference frame. In the current study, we have found a reduced ability in old adults to exploit the egocentric reference frame for self-motion perception, as opposed to verticality perception, as indicated by the age effect on natural drift. As mentioned above, this is likely due to age effects on somatosensation. In addition to reduced proprioceptive acuity with age (Goble, 2009; Hurley et al., 1998), brain structures linked to proprioceptive acuity such as the putamen have been shown to suffer age effects (Goble, 2011). Furthermore, age-related somatosensory deficits have been linked to a reduced ability to exploit the egocentric reference frame for spatial orientation in terms of constructing and updating one's internal models (Barbieri et al., 2010; Boisgontier & Nougier, 2013). Studies have demonstrated an association between activation in parietal brain regions and the construction and maintenance of the egocentric reference frame in terms of an internal representation of the self (Bottini et al., 2001; Hagura et al., 2007; Vallar et al., 1999; Wolpert, Goodbody, & Husain, 1998). This region is

particularly susceptible to aging, as shown by large differences in grey matter between young and old adults (Good et al., 2001; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003). It appears therefore that exploitation of the egocentric reference frame is compromised in old adults due to both peripheral sensory and central decline.

Finally, the poorer sensory reweighting ability in older adults should be mentioned. Several studies have revealed a reduced capacity to shift reliance from one reference frame to another with age as well as adaptation difficulties to new or perturbing sensory environments (Bugnariu & Fung, 2007; Eikema et al., 2012; Eikema, Hatzitaki, Konstantakos, & Papaxanthis, 2013; Slaboda et al., 2011; Slaboda & Keshner, 2012). These reports have established a link between increased reliance on the visual reference frame and reweighting difficulties in old adults. Our results support these findings and extend the premise of reweighting difficulty to also be associated with poorer egocentric self-motion information exploitation.

III.4.3 Postural orientation versus self-motion perception

Self-motion and self-orientation perception in space are components contributing to the maintenance of equilibrium. Motion and postural orientation are tied under quiet standing, given that when the feet remain stationary any motion is due to body lean. When walking, running or stepping in place, however, the two are not necessarily linked as closely. During simple translation, for example, one's body movements may not lead to large changes in segmental orientation with respect to the vertical. In addition, the mechanical differences tied to stance and walking lead to different structures of the generated optic flow. In our protocol, we used linear ground optic flow in order to examine the translational component of a visual stimulation that provides information on one's self motion speed and direction under locomotion. In quiet stance the optic flow generated is typically oscillatory, which is why oscillatory stimuli are often employed when examining the contribution of dynamic cues to postural control (Bardy, Warren Jr, & Kay, 1996; Borger et al., 1999; Dijkstra, Schöner, & Gielen, 1994; Eikema et al., 2012; Hanssens, Allard, Giraudet, & Faubert, 2013; Keshner & Kenyon, 2000; Lee & Lishman, 1975; Stoffregen, 1985). In these studies, participants experienced the oscillatory flow as if it were due to their own movements and therefore swayed in the same direction as the stimulus to cancel the difference in perceived self-motion speed. Directional postural responses have also been observed in studies employing linear flows however (Baumberger et al., 2004; Holten, Donker, Verstraten, & van der Smagt, 2013; Lestienne, Soechting, & Berthoz, 1977; Bronstein, 1986; Sundermier et al., 1996; Palmisano, Pinniger, Ash, & Steele, 2009; Wei, Stevenson, & Körding, 2010; Berthoz, Lacour, Soechting, & Vidal, 1979).

We hypothesised that optic flow direction would influence head and trunk pitch during quiet stance as observed in the literature. Moreover, we expected to observe differences in age groups as well, possibly

revealing a precautionary postural strategy in older adults to avoid the risk of falling given that, ultimately, the visual perception of approaching or receding flows when standing may be associated with a fall. However, we observed neither an age effect, nor an optic flow direction effect on head pitch orientation, only the trunk moved backwards under approaching flow compared to the other visual stimulation conditions. It is possible that the more ecological approaching flow was a stronger stimulus and therefore the trunk followed the head re-orientation, while this was not observed under receding flow. Interestingly, we observed a common response of the head to both dynamic visual stimuli, tilting backwards compared to under the static stimulus for both postural tasks. This behaviour may reflect a stabilisation strategy to minimise the sensory perturbation and conflict between visual and non-visual information under the optic flow conditions. Tilting the head backward reduces the visual ground stimulus on the retina in addition to reducing the sensitivity of the vestibular system (Brandt, Krafczyk, & Malsbenden, 1981; Della Santina, Potyagaylo, Migliaccio, Minor, & Carey, 2005; Schubert, Tusa, Grine, & Herdman, 2004). This stabilisation hypothesis is supported by the results on stepping frequency and step width which increased under both optic flow conditions while stepping in place compared to static stimulation. Increase of stepping frequency and step width are strategies that improve equilibrium maintenance by reducing lateral instability, which has been shown to be greater than anteroposterior instability while walking (O'Connor & Kuo, 2009) and especially for old adults (Franz et al., 2015; Yeh et al., 2014). By increasing both stepping frequency and step width, the weight transfer from one leg to the other is limited and therefore so are postural orientation changes, including mediolateral head movement (which would compromise information gathering and processing). In addition, old adults showed increased stepping frequency compared to the other two age groups. This result is in agreement with the aforementioned increased visual sensitivity with age, with old adults demonstrating a cautionary postural control strategy under visual perturbation. Furthermore, total translation results during quiet stance further corroborate this observation in old adults. Old adults appeared to respond on average with a backward translation under any visual perturbation while this was forward for the young. Contrary to head pitch orientation however, an optic flow direction effect was observed on this kinematic variable. All groups moved further forwards under receding flow compared to static stimulation and approaching flow. Approaching flow is more common in everyday life than receding flow which could explain the difference in visual stimulation effect between the two flows and the static stimulus. It may be that compensation mechanisms were put into action in order to limit translation under approaching flow while receding flow 'pulled' participants forwards – or kept them from being 'pushed' further back, in the case of old adults.

Our optic flow stimuli were projected on a relatively small (4.8 m x 1 m) portion of the ground thereby providing only a limited immersive experience compared to previous studies examining effects of spatially endless ground optic flow (Baumberger, Isableu, & Flückiger, 2004; Flückiger & Baumberger, 1988). Nevertheless, directional optic flow effects were observed in the kinematic variables. It appears therefore that the dynamic stimuli were potent enough to influence body kinematics depending on direction, but not alter postural orientation (at least for the head). The ground being an invariant source of information for self-motion and spatial orientation, it is noteworthy that old adults were a) less able to exploit the somatosensory

invariance tied to this support surface while stepping in place and b) more influenced by the visual motion of the ground, and this for both approaching and receding flow.

The distinction between exploitation of the egocentric reference frame in terms of self-motion perception as opposed to spatial orientation should be highlighted. Postural orientation establishes a postural reference both with respect to the external environment and between segments (Kluzik et al., 2007). Keshner and Kenyon (2000) discuss the fact that when actively moving in the environment, somatosensory feedback from the podal contacts with the support surface combine with otolith signals to provide information about the stability of the base of support. When faced with incongruent dynamic visual stimuli, this combined information weighs the correct perception of verticality more heavily, reducing the influence of the visual environment. In contrast our results indicated that the intermittent podal contact when stepping in place may actually attenuate somatosensory information on self-motion perception with respect to the ground surface, facilitating the influence of ground optic flow information. The difference lies in the *purpose* of exploiting the egocentric reference frame, i.e. to construct the postural orientation reference versus the body motion reference. Intrigued, we examined the relationship between natural drift and RBT scores. Although significant, the correlation was relatively weak (R^2=0.11, p=0.014). It seems therefore that exploitation of the egocentric reference frame for spatial-orientation and self-motion perception may be different, though in both cases it is associated with increased optic flow sensitivity.

III.5 Conclusion

In conclusion, our study has revealed that self-motion perception with respect to the ground is achieved by relying on visual rather than somatosensory information in old adults. The greater natural drift observed in old adults may be a sign of reduced ability to exploit the egocentric frame of reference, possibly due to age-related somatosensory deficits. In addition, the inability to disambiguate visual from egocentric self-motion cues is evident from middle age. This is demonstrated by the fact that middle-aged and old adults drifted backwards while stepping in place under approaching flow compared to the static stimulus and receding flow, while young adults showed no significant difference in translation between visual conditions. Moreover, stepping in place proved to be a simple yet effective means to examine how ground optic flow influences postural behaviour, especially in old adults. Indeed the intermittent contact with the ground surface seems to have enhanced the directional effects of ground optic flow by affecting body-on-support perception. Finally, the COVR (visual self-motion quotient) appears to be an appropriate motor index of reliance on the visual reference frame as it revealed: a) greatest directional sensitivity to ground optic flow, b) increased sensitivity in old adults in agreement with the literature, and c) significant correlations with visual (positive) and egocentric (negative) reference frame reliance for spatial orientation and self-motion perception.

IV. *Chapter 4: Optic flow influence while walking – aging and reference frame reliance*

IV.1 Introduction

The last experimental chapter focuses on the influence of ground optic flow on the control of walking. Walking requires the appropriate sampling and integration of different types of sensory information. Visual, vestibular and somatosensory inputs must be appropriately weighted and dynamically reweighted depending on the environment and walking task difficulty, for example when walking in a crowded setting or on riskier surfaces (e.g. slopes, uneven terrain, slippery ground). Sensory, motor and central processes degrade with old age and motor control is subjected to increased noise at every level of the nervous system and to longer processing and execution timeframes. This renders simple ambulation a more physically and cognitively demanding task (see Seidler et al., 2010 for a review). Moreover, old adults are more prone to falling as 30% of those over 65 fall at least once a year (Tinetti, Speechley, & Ginter, 1988; Campbell, Reinken, Allan, & Martinez, 1981; O'Loughlin, Robitaille, Boivin, & Suissa, 1993). Falls are thus a major public health issue, leading to loss of autonomy and are an established cause of morbidity among senior citizens. In addition, studies have revealed visual field dependence as a risk factor for falling in old adults (Barr et al., 2016; Lord & Webster, 1990). Having previously established that our older participants were more reliant on the visual frame of reference and subsequently revealed an indicator of reliance on ground optic flow while stepping in place (visual self-motion quotient), our aim here was to examine whether signatures of visual field dependence, or more specifically, reliance on ground optic flow, could be identified while walking. The novelty here would be how to distinguish a greater reliance on the visual FoR from the known influence of optic flow on the control of walking (i.e. regardless of preferred modes of spatial referencing).

When moving through an environment, optic flow provides information on self-motion speed and direction. Manipulating the focus of expansion or speed of an optic flow stimulus has been shown to, respectively, generate alterations in one's heading direction (Berard et al., 2009; Berard et al., 2011; Sarre, Berard, Fung, & Lamontagne, 2008; Saunders & Durgin, 2011; Warren et al., 2001) and walking speed (Baumberger et al., 2000; De Smet et al., 2009; François et al., 2011; Mohler, Thompson, Creem-Regehr, Pick Jr, & Warren Jr, 2007; Pailhous et al., 1990; Prokop et al., 1997; Varraine, Bonnard, & Pailhous, 2002). Although variability has been observed, revealing a continuum in the relative impact of optic flow manipulations on gait (Poulain, Gaignard, Marin, Mantel, & Bernardin, 2015), it is generally accepted that providing artificial optic flow, i.e. visual self-motion information, that is incongruent to the self-motion perceived via somatosensory and vestibular cues, leads to the adjustment of one's walking pattern in order to minimise the sensory discordance and thus adapt to the movement specified by the optic flow.

The exacerbated reliance on the visual frame of reference and associated reduced ability to appropriately reweight sensory cues of old adults (Eikema et al., 2012; Eikema et al., 2013) would lead us to assume that this population would be less able to adjust their gait pattern when faced with artificial optic flow, in order to minimise the induced sensory discordance and maintain stability. Studies have shown, however, that the guiding effect of optic flow on gait classically observed in young adults is preserved with age (Chou et al., 2009; Schubert et al., 2005; Konczak, 1994; Lamontagne, Fung, McFadyen, & Faubert, 2007). Moreover, no age differences have been found between young and old adults in terms of optic flow-induced modulations in locomotor parameters (Chou et al., 2009; Schubert et al., 2005; Konczak, 1994). Konzcak (1994) has highlighted, however, the great amount of variability within the old adult group of his study which may have contaminated his statistical analysis. Furthermore, in the Chou et al. (2009) study, old adults were not significantly more visual field dependent, as indicated by comparable scores on the rod and frame test between the two age groups. On the contrary, in our group of old adults, greater reliance on the visual frame of reference has been established in terms of both spatial orientation and self-motion perception, therefore we may indeed expect to observe differential effects of ground optic flow between age groups. It is also possible, however, that such gait variables are not sensitive to the differential reweighting of sensory cues between young and old adults or, incidentally, between less and more visual field dependent individuals respectively.

Examining postural control via strategies of body segment stabilisation may be more appropriate in order to observe a differential reliance on the visual FoR while walking. This has been done in children and Parkinson's disease (PD) patients, given that these individuals are considered more reliant on visual and especially, dynamic visual cues (Assaiante & Amblard, 1992; Azulay et al., 1999; Azulay et al., 2002). By examining the anchoring index (AI) between adjacent segments (Amblard, Assaiante, Fabre, Mouchnino, & Massion, 1997; Assaiante & Amblard, 1993), studies revealed that children (Assaiante & Amblard, 1993) and PD patients (Mesure, Azulay, Pouget, & Amblard, 1999) used a rigid, *en bloc* segmental stabilisation strategy in order to limit the relative degrees of freedom between segments, as opposed to a more articulated strategy in order to maintain balance. It has been suggested that stabilising the head in space in particular, allows for a better processing of visual and vestibular sensory feedback in order to maintain balance. In addition, a more rigid segmental stabilisation strategy has been observed in old adults with a higher risk of fall during turning (Wright et al., 2012). The old adult controls in the Mesure et al. (1999) study showed no preferred head stabilisation strategy, i.e. neither systematically in space nor systematically on the underlying trunk segment, the analysis, however, was performed without any visual perturbations, therefore in a natural setting. Differential behaviour with regard to reliance on the visual reference frame may be observed under conditions of visual versus egocentric information incongruence in healthy adults. Indeed, under visual perturbations, young visual field dependent individuals have been shown to use the *en bloc* strategy in postural control (Isableu et al., 2003), while their visual field independent counterparts showed an articulated segmental stabilisation strategy.

In this chapter therefore, we extended the examination of differential ground optic flow influence on our three age groups' behaviour from orientation and translation, as seen in the previous chapter, to segmental stabilisation. We utilised both approaching and receding flow in order to examine ground optic flow direction effects across our population. As we saw in the previous chapter, our old adults were more sensitive to optic flow and less able to exploit egocentric information for self-motion perception. We could therefore assume that the visual incongruence provided would perturb these participants' stability while walking. We examined both the initial gait cycle and steady state gait. Many falls are reported to occur in old adults when initiating gait (Winter, 1995) as it is a task of transition from standing, a relatively static posture, to a dynamic and cyclical motion and therefore imposing greater requirements for balance control than during steady state gait (Polcyn, Lipsitz, Kerrigan, & Collins, 1998; Assaiante, Woollacott, & Amblard, 2000). Indeed, old adults are more variable in their head and trunk during the initial gait cycle orientation and show a more rigid head-trunk unit (Laudani et al., 2006). We thus hypothesised that, firstly, any differences between the initial gait cycle and steady state gait would be more evident in old adults and, secondly, that it may be only during the initial gait cycle that an age-specific response to optic flow would occur. Given that the walking tasks presented in this chapter followed from the postural tasks described in Chapter 3, we chose to analyse the AI in both postural (QS and SIP) and walking tasks in order to examine the influence of the motor task on the head stabilisation strategy, in addition to the interaction with the visual stimulation provided. We also examined basic locomotor parameters: step length, step width, stepping frequency and walking speed. Our rationale was that although studies have not found differential gait modulations between young and old adults, the influence of the visual stimulation immersion period may reveal age-related differences. It is possible that the optic flow influenced mainly the postural tasks, the effect diminishing over the 30 s period preceding the initiation of gait. Considering, however, old adults' slower reweighting and adaptation capacities, we may observe a greater modulation in the gait parameters of old adults compared to the younger participants since the effect would not have diminished for the older participants as much as for the younger ones.

IV.2 Methods

The protocol presented in the previous chapter was a segment of the experiment carried out. Participants, set-up (see Figure III.1a) and stimulus pattern were all identical with the experimental procedure of Chapter 3. The extended procedure is presented below to include the walking tasks that followed the postural tasks of Chapter 3.

IV.2.1 Procedure

At the beginning of the session, a control walking condition was completed. Each participant was instructed to walk naturally, at a preferred and habitual pace across the 5 m walkway while looking straight ahead. Room lights were on and no stimulus was projected onto the walkway. Three trials were recorded. Walking speed was calculated over the second gait cycle by dividing the distance travelled by the sternum marker by the time taken to travel that distance. Preferred walking speed was estimated as the mean of the three trial measurements and subsequently used to calculate the optic flow speeds used for that participant.

After standing quietly (QS) or stepping in place (SIP) on the force plate for 30 s, participants were instructed to walk at their preferred walking speed across the 5 m of the walkway in front of them while looking straight ahead. No fixation point was provided. Quiet standing and stepping in place tasks were counterbalanced for each participant to avoid fatigue. Each experimental session began with the visual condition of natural flow (NF), then static stimulation (ST) in order to avoid any visual motion after effect. Two ground optic flow direction conditions were subsequently recorded: approaching (AF), and receding flow (RF). The order of the optic flow direction conditions were randomised between participants. All conditions were performed in blocks of five trials. Trials will be referred to as QS-first or SIP-first to distinguish them with respect to the initial postural task and thus allow an analysis of the possible effect of the initial postural conditions on the subsequent walking. Projection of the visual stimulus and data acquisition were stopped before participants reached the end of the walkway to avoid recording the deceleration due to gait termination. In total 2 initial postural tasks x 4 visual stimulation conditions x 5 trials were completed.

The instructions were given before each block of five trials. Set breaks were taken every four blocks of trials to avoid fatigue. With preparation and brakes included, the experiment duration averaged 2 hours.

IV.2.2 Optic flow stimuli

The optic flow stimuli had gains, *g*, corresponding to -0.5 and +0.5 for approaching and receding flows respectively. To account for the natural optic flow occurring when humans move in their environment, the flow velocity was modified when participants walked off the force plate, upon gait initiation. The flow speed whilst on the force plate was computed as

$$v_{OF} = v_W * g \qquad \text{(IV.1)}$$

and when walking across the walkway as

$$v_{OF} = v_W * (g + 1) \quad \text{(IV.2)}$$

where v_{OF} is the optic flow speed, v_W is the participants' average preferred walking speed and g is the visual gain. In this way, we attempted to maintain the same visual gain between the postural and walking tasks. Indeed, when asked at the end to the experiment, few participants reported noticing the gain change when stepping onto the walkway.

IV.2.3 Data processing

Motion capture and force plate data were filtered with a second order low pass Butterworth filter with a cut off frequency at 3 Hz. To account for slight differences in trial lengths due to the reaction times associated with the instruction for participants to move forwards, and for the difference in sampling frequency between the motion capture system (100 Hz) and force plate (500 Hz), all signals for the period on the force plate were resampled to 3000 frames, corresponding to 30 s with a sampling frequency of 100 Hz. Two periods were established for walking data analysis: the initial gait cycle and steady state gait. A start time, t_{start}, was established for both QS-first and SIP-first trials as the time point from which gait data were analysed. A gait cycle is defined as the period from a heel strike to the next heel strike of the same (ipsilateral) foot. The initial gait cycle was analysed separately and was defined as the period from t_{start} to the second occurring heel strike. For steady state gait, indices were calculated per gait cycle and means and standard deviations determined over the number of cycles recorded.

The onset of anticipatory postural adjustment (APA) prior to gait was defined as t_{start} for QS-first trials. To detect the APA onset, heel off times were first detected. For this, we established the time point, t_{toe}, when the first of the two toe markers moved beyond the forward edge of the force plate. A threshold was set in the vertical (z) axis for heel elevation acceleration, defined as the mean plus 4 times the standard deviation of the acceleration signal of the two heel markers over a period of 6 s up until 2 s prior to t_{toe}. Whichever marker passed this threshold first marked the heel-off time, t_{HO}, for gait initiation. The threshold for APA onset detection was defined as the mean plus 4 times the standard deviation of the COP acceleration (Martinez-Mendez et al. 2011) over an interval of 20 s up to 2 s prior to t_{HO}. The APA onset was defined as the first time point when the COP acceleration signal passed this threshold in a window of 2s prior to t_{HO}. Figure IV.1 illustrates the COP acceleration and heel elevation signals within a QS-first trial indicating APA onset and initial heel off times. In the literature, both the mediolateral (ML) and anteroposterior (AP) COP signals are used for APA detection. To account for possible effects of age or visual condition on APA, we established t_{start} as the earlier of the AP or ML APA onset time points.

For SIP-first trials, gait initiation was identified by detecting the first heel to accelerate forwards on the anteroposterior axis beyond a threshold defined as the mean plus 4 times the standard deviation of the heel acceleration signal in the AP axis, over a period of 4 s prior to the 30 s mark of the time spent on the force plate. The last heel strike prior to gait initiation was defined as t_{start}. Heel strike times were identified for each heel by evaluating when the velocity signal of the heel in the vertical axis changed sign. This applied to stepping in place as well as walking data. Automatic detection of the above events was manually validated or corrected when necessary for each trial. All data processing was performed with in-house scripts using Matlab.

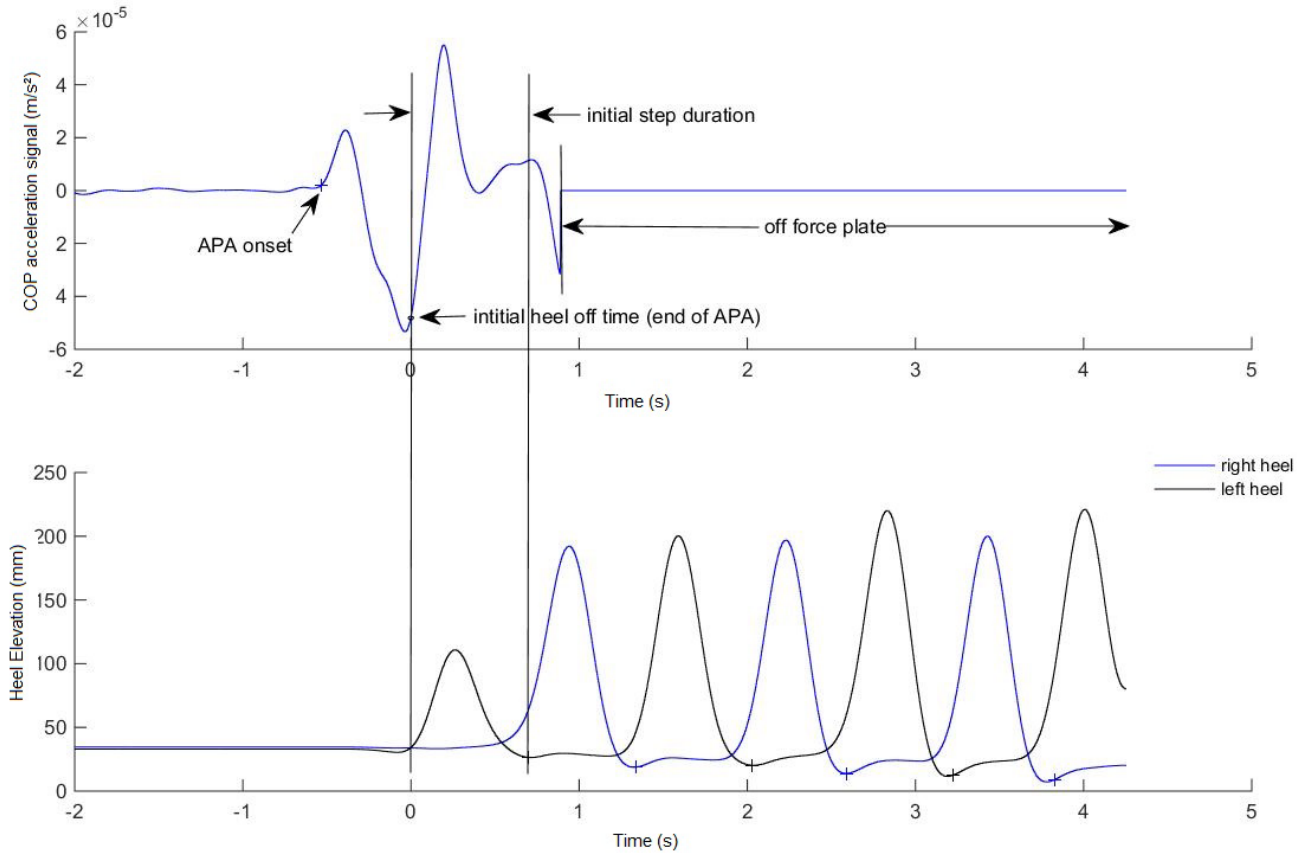

Figure IV.1 Example of t_{start} detection (APA onset) for QS-first trial. Time=0 is the heel-off time, t_{HO}. Top: COP acceleration signal in the antero-posterior direction. Bottom: Heel position signal on vertical axis for both feet, crosses mark heel strike times.

IV.2.4 Dependent variables

IV.2.4.1 *Locomotor parameters*

Step length, width, frequency and walking speed were calculated for the initial gait cycle and average of steady state gait cycles. Step length was defined as the Euclidian distance between the heel of the trailing foot to the heel of the leading foot (in cm). Step width was defined as the mediolateral distance between the heels of the two feet (in cm). Step frequency was calculated based on the time between heel strikes and converted to the number of steps per minute and walking speed was measured by taking the distance travelled by the centroid of the head over the stride duration (m/s).

IV.2.4.2 *Head and trunk orientation and stabilisation*

Head and trunk angles were calculated in the three rotation planes. The method of calculation and analysis is fully described in Chapter 3. We used the convention of 90° defining the vertical orientation for pitch, upright for roll and straight ahead for yaw. The orientations calculated were relative to the control condition: quiet standing with arms hanging on the sides, feet hip-width apart while participants looked straight ahead. A 90° angle therefore, in any plane signified that the participant's orientation was identical to the one recorded during the reference measurement for that plane. Angles below 90° indicated down/forward pitch or rightward roll/yaw and inversely, angles above 90° indicated up/backward pitch and leftward roll and yaw, see Figure IV.2 below. Given that our stimuli were in the sagittal plane, we focused our analysis on pitch rotation for mean head and trunk orientation modulations.

For a first index of segmental stability, the amplitude of head and trunk oscillations were evaluated in all three planes to assess whether stability was achieved in other planes (refs) than the one stimulated by the projected ground optic flow. This index was simply the standard deviation of head and trunk orientation in each plane calculated during the initial gait cycle or steady state gait of a given trial.

Head stabilisation strategy was defined in terms of the *anchoring index* (AI). This index represents how the head and trunk move relative to one another, i.e. whether the head is stabilised independently (head stabilisation in space) or anchored to the trunk (head and trunk are *en bloc*). The AI was determined for pitch and roll angles and defined as:

$$AI = \frac{\sigma^2_{rel\_head} - \sigma^2_{head}}{\sigma^2_{rel\_head} + \sigma^2_{head}} \quad \text{(IV.3)}$$

where σ_{head} is the standard deviation of the head angle (in pitch or roll) and σ_{rel_head} is the standard deviation of the head relative to the trunk angle (in pitch or roll). A positive AI indicates an articulated strategy with the head stabilised in space whereas a negative AI indicates a rigid, *en bloc* strategy with the head stabilised on the trunk. As opposed to the other indices for steady state gait, the AI was calculated over the entire steady state gait period and not averaged across gait cycles.

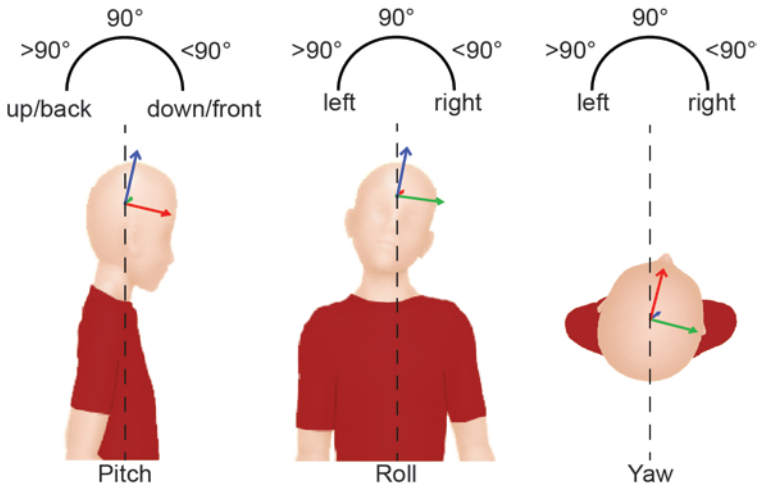

Figure IV.2 Illustration of convention used for pitch, roll and yaw rotation angles, indicated at the level of the head.

IV.2.5 Statistical analysis

Means and standard deviations of all indices were calculated over the five trials for each participant. For the locomotor parameters, head and trunk orientation (in pitch) and oscillation amplitudes (in all three rotation planes), we subtracted the value obtained under the natural flow condition (control) from the other three stimulation conditions in order to obtain relative measures.

We first examined the control values (baseline) for the locomotor parameters and segmental data with an initial postural task (2) x gait cycle (2) x age group (3) repeated measures ANOVA. In order to focus on visual stimulation and not consider baseline differences for age groups, values relative to the control condition were used under the conditions of imposed visual stimulation. The relative values for the above indices were evaluated next with an initial postural tasks (2) x gait cycle (2) x visual stimulation (3) x age group (3) repeated measures ANOVA. Given that the anchoring index is a variable qualifying the preferred

head stabilisation strategy depending on the value difference with respect to zero, we could not analyse values relative to the control condition under the conditions of imposed visual stimulation, and therefore all four visual stimulation conditions were included in the ANOVA plan. The AI data were evaluated separately for the postural and walking tasks. Given the large variability between quiet standing and stepping in place, a visual stimulation (4) x age group (3) ANOVA was performed for each postural task. For the walking data, an initial postural condition (2) x gait cycle (2) x visual stimulation (4) x age group (3) repeated measures ANOVA was performed. The partial eta squared (η^2) was used to determine effect strengths for the ANOVAs. Tukey's honest significant difference (HSD) test ($p < 0.05$) was used for *post hoc* comparisons. Given that the AI values are limited between -1 and +1, the data were converted using a z-transform in order to follow a Gaussian distribution. T-tests were performed on the AI data to compare values to zero and thus qualify the head stabilisation strategy adopted.

IV.3 Results

IV.3.1 Main findings

In this section the main findings are summarised to provide a global view of our results, these are subsequently detailed in the next section.

Gait modulation and segmental pitch re-orientation

We first examined baseline differences between our three age groups by analyzing the locomotor parameters and head and trunk mean pitch orientations in the control condition, i.e. under natural flow, these are illustrated in Figure IV.3. Means and standard deviations are provided in Tables VI.1 and VI.2 (cf., Appendix 2, pp 137, 138). Our main findings showed that old adults 1) walked more slowly and took shorter steps, which is commonly reported in the literature and 2) had a lower mean head pitch orientation than the other age groups and especially during the initial gait cycle (see Figure IV.7).

Optic flow influenced walking speed, step length and stepping frequency as may be seen in Figures IV.4, IV.5 and IV.6 respectively. There was also an influence of optic flow on head and trunk mean pitch orientations as may be seen in Figures IV.8 and IV.9 respectively. Our main findings with respect to visual stimulation indicated that 1) walking speed was reduced under approaching flow while step length was

reduced under both optic flow conditions and stepping frequency increased under receding flow and 2) mean head pitch orientation was greater under both optic flow conditions while, depending on the initial postural condition and gait cycle, a directional effect was found on mean trunk pitch orientation indicating forward lean under receding flow and backward lean under approaching flow.

Differences between age groups were found under the imposed visual stimulation conditions for stepping frequency and mean head and trunk pitch orientation. The results we observed revealed that old adults 1) increased their stepping frequency compared to the other two age groups, 2) tilted their head further back during the initial gait cycle under both optic flow conditions compared to steady state gait and 3) tilted their trunk further back under approaching flow and further forwards under receding flow, all walking cycles and trials combined, while this was not significant for the other age groups.

Head and trunk stability

Head and trunk stability were evaluated via the mean amplitude of oscillations about each rotation plane while the head-trunk anchoring index examined participants' head stabilisation strategy (in space vs. on the underlying trunk segment). Mean oscillation amplitude values during the control conditions are provided in Figure IV.10, while means with standard deviations are also included in Table VI.2 (cf., Appendix 2, pp 138). We found that old adults had smaller amplitudes of head oscillations in roll and of trunk oscillations in all three planes compared to the younger participants.

Examining these indices under conditions of imposed visual stimulation, we observed that the influence of the visual stimulus on head and trunk stability depended on the initial postural condition and gait cycle as will be elaborated in the next section. Head oscillation amplitudes were reduced under optic flow (see Figure IV.11) while trunk oscillation amplitudes increased under receding compared to approaching flow (see figure IV.12). However, no differences between age groups were observed.

Finally, we considered head stabilisation strategy across postural and walking tasks, visual stimulation conditions and age groups in pitch (Figure IV.13) and in roll (Figure IV.14). The following findings emerged:

1) during the quiet standing (QS) postural task, all participants showed an *en bloc* head stabilisation strategy under all visual stimulation conditions
2) old adults had lower AI values compared to the younger participants
    a. in both pitch and roll during the stepping in place (SIP) postural task
    b. in pitch during the initial gait cycle

3) head stabilisation in space improved under imposed visual stimulation conditions compared to the control condition during SIP and walking in both pitch and roll

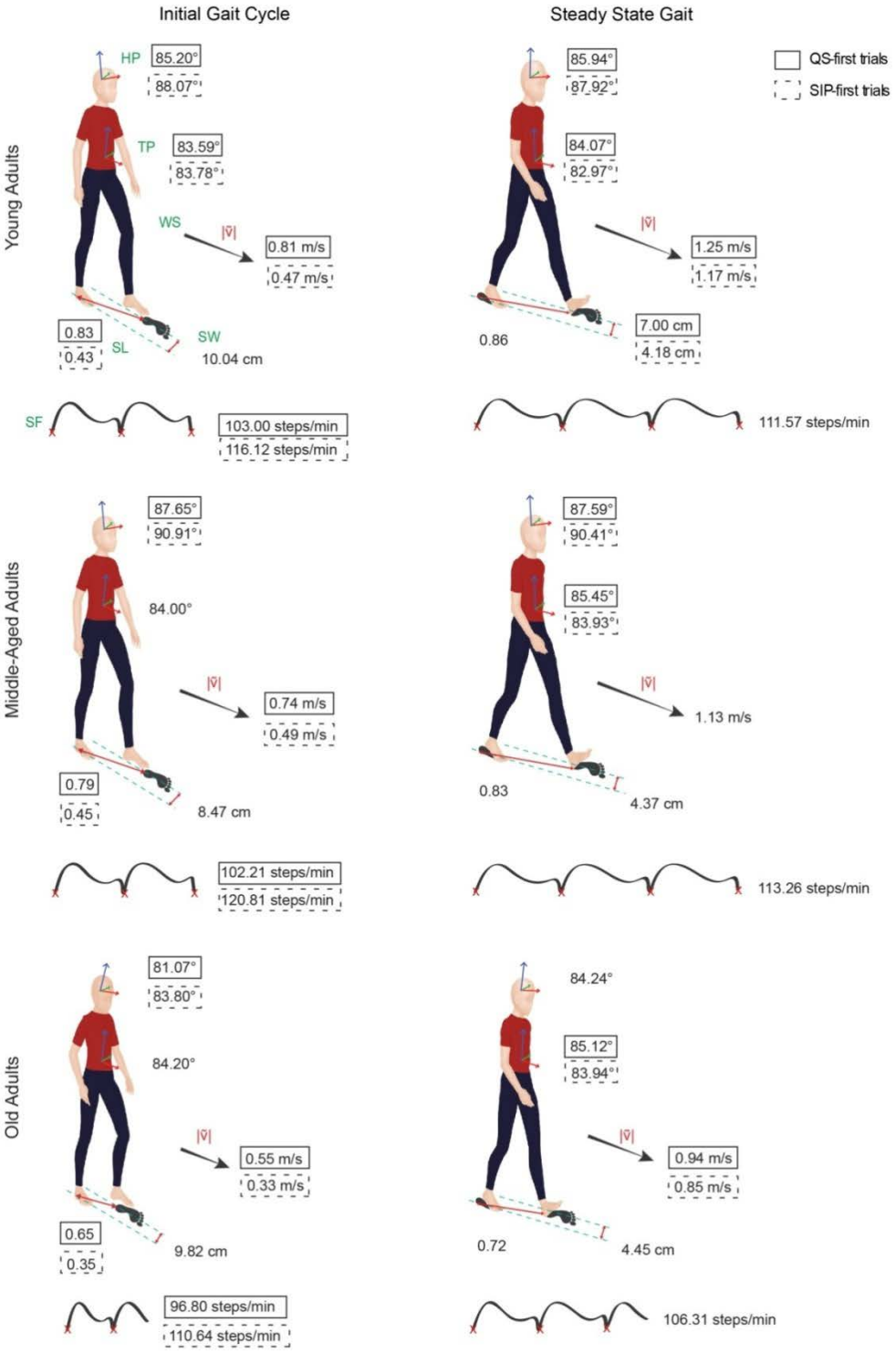

Figure IV.3 Schematic illustration of baseline values for mean head and trunk pitch orientations and locomotor parameters for each age group during the initial gait cycle (left) and steady state gait (right). If values differed significantly between QS-first and SIP-first trials both values are provided within a solid or dashed frame respectively, otherwise the average value is indicated. HP: mean head pitch orientation; TP: mean trunk pitch orientation; WS: walking speed; SL: normalised step length; SW: step width; SF: step frequency.

We shall now consider these main results in more detail.

IV.3.2 Detailed presentation of our results

While we are conscious that the postural tasks preceding walking may influence the parameters we evaluated, our focus is on the influence of visual stimulation in the context of ageing, therefore unless interactions were observed with the visual stimulation condition or age group, we shall not report effects of initial postural condition. The same applies for differences between gait cycles. The initial gait cycle differs from steady state gait, but such differences are beyond the scope of our work unless these depended on the visual stimulation condition or age group.

IV.3.2.1 ***Locomotor parameters***

We first considered the locomotor parameters between our three age groups, the means of the four indices examined are presented schematically in Figure IV.3. A main effect of age group was found for step length ($F(2, 53)=13.90$, $\eta^2= 0.34$, $p=0.000$) and walking speed ($F(2, 53)=23.16$, $\eta^2= 0.47$, $p=0.000$). Tukey's HSD *post hoc* test revealed significant reductions in both step length and walking speed in old adults compared to middle-aged and young adults ($p<0.05$). Moreover a triple interaction effect (initial postural condition vs. gait cycle vs. age group) was found for both step length ($F(2, 53)=5.87$, $\eta^2= 0.18$, $p=0.005$) and walking speed ($F(2, 53)=7.32$, $\eta^2= 0.22$, $p=0.002$). Interestingly, gait cycle and initial postural condition influenced the manifestation of age group effects on step length. For this variable the age group differences appeared during the initial gait cycle of QS-first trials and during steady state gait of SIP-first trials ($p<0.05$) as revealed by a triple interaction effect ($F(2, 53)=5.87$, $\eta^2= 0.18$, $p=0.005$). Moreover only the old adults showed a shorter step length during the initial gait cycle compared to steady state gait in QS-trials while for SIP-first trials the cycle difference was observed in all three age groups ($p<0.05$). We may therefore infer that the act of stepping in place conditioned the subsequent initiation of gait leading all participants to behave in a similar manner. More specifically, in order to adjust the stepping pattern from minimal anteroposterior translations to stepping in order to move forwards, all participants would have to produce the same transition thus eliminating individual differences due to age during the initial gait cycle. This adjustment being common to all participants explains the difference in step length between gait cycles, while initiating gait from quiet stance required taking shorter steps compared to during steady state gait only for old adults. For stepping frequency only a trend was found ($F(2, 53)=3.07$, $\eta^2= 0.10$, $p=0.055$) whereby old adults walked at a reduced stepping frequency of 105.01 steps/min compared to middle-aged and young adults, with means of

112.38 steps/min and 110.56 steps/min, respectively. While no age differences were found for step width, an initial postural condition vs. gait cycle vs. age group interaction effect ($F(2, 53)=3.83$, $\eta^2=0.13$, $p=0.028$) for step width revealed that young adults reduced their step width during steady-state gait of SIP-first compared to QS-first trials ($p<0.05$).

We next examined step length, width, frequency and walking speed relative to the control condition under the influence of imposed visual stimulation, that is static stimulation, approaching and receding optic flow. Main effects of visual stimulation were found for walking speed ($F(2, 106)=4.20$, $\eta^2=0.07$, $p=0.018$), step length ($F(2, 106)=5.68$, $\eta^2=0.10$, $p=0.005$) and step frequency ($F(2, 106)=3.96$, $\eta^2=0.07$, $p=0.022$) as indicated in Figures IV.4, IV.5 and IV.6 respectively. Tukey's HSD tests revealed that walking speed was significantly slower only under approaching flow compared to static stimulation while step length was reduced under both optic flow conditions compared to static stimulation and step frequency increased under receding flow compared to static stimulation and approaching flow ($p<0.05$). Receding flow being less common may have led our participants to adopt a greater stepping frequency alongside the reduction in step length in order to maintain a comfortable walking speed (no modulation observed for this variable under receding flow) and hence preserve stability. A main effect of age group ($F(2, 53)=6.88$, $\eta^2=0.21$, $p=0.002$) was found only for step frequency, indicating that old adults significantly increased their stepping frequency compared to both young and middle-aged adults ($p<0.05$). No significant effects of visual stimulation, age group, initial postural condition or gait cycle were found for step width.

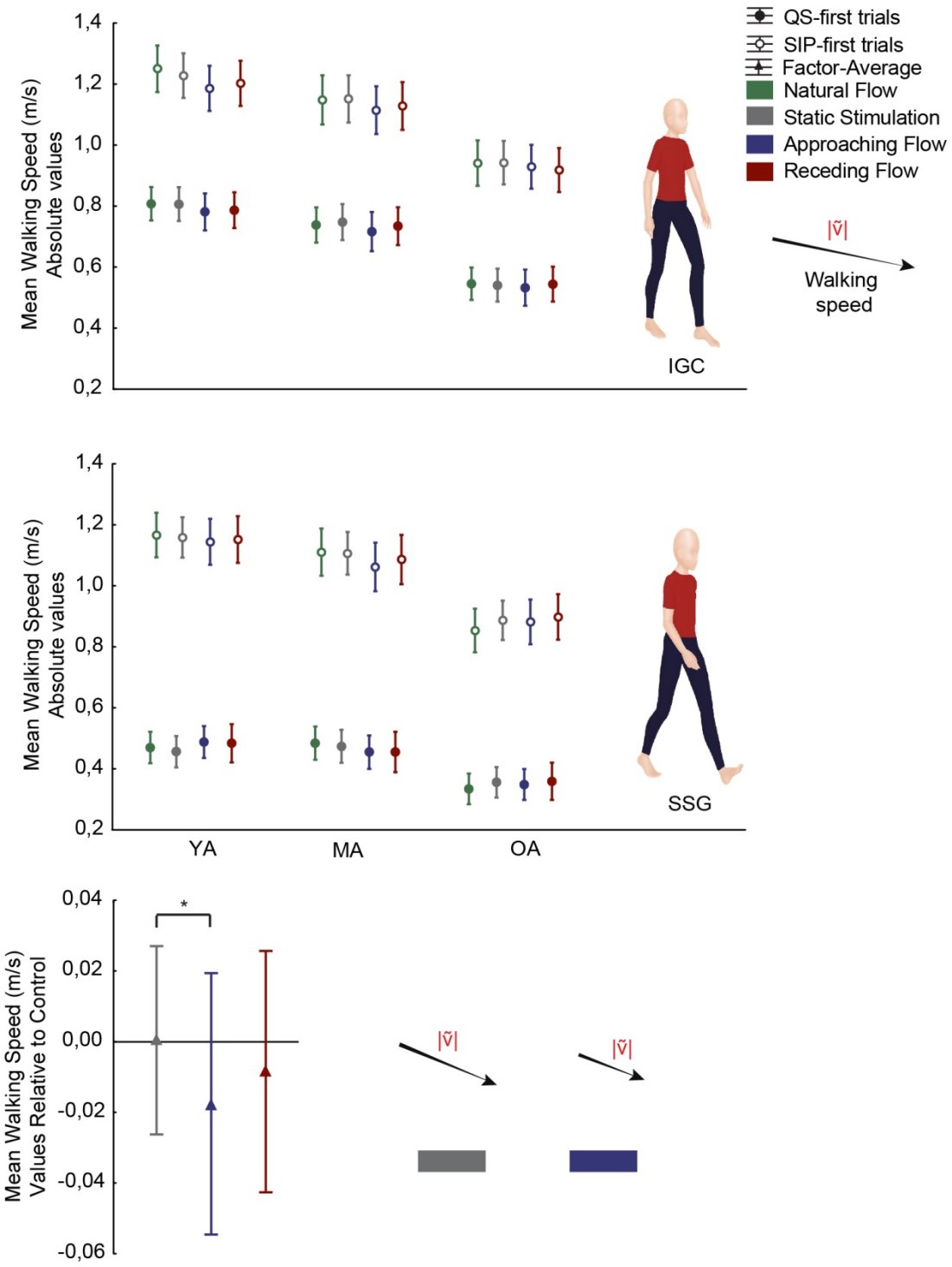

Figure IV.4 Absolute values of mean walking speed across visual stimulation conditions for both trial types in each age group during the initial gait cycle (top) and steady state gait (middle). Bottom: Values relative to the control condition, pooled across gait cycles, trial types and age groups revealing the main visual stimulation effect illustrated on the right. Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

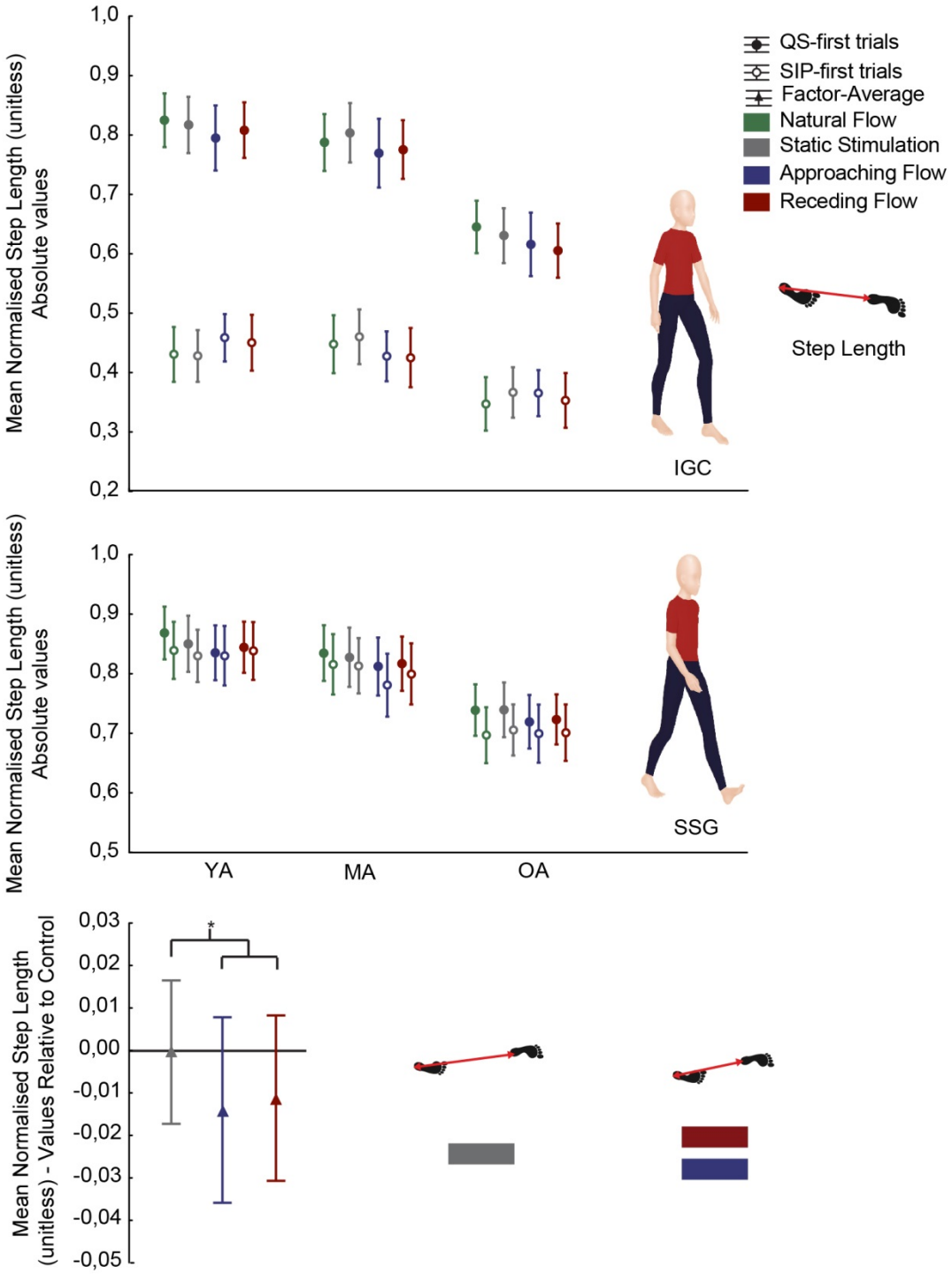

Figure IV.5 Absolute values of mean normalised step length across visual stimulation conditions for both trial types in each age group during the initial gait cycle (top) and steady state gait (middle). Bottom: Values relative to the control condition, pooled across gait cycles, trial types and age groups revealing the main visual stimulation effect illustrated on the right. Error bars indicate 95% confidence intervals.YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

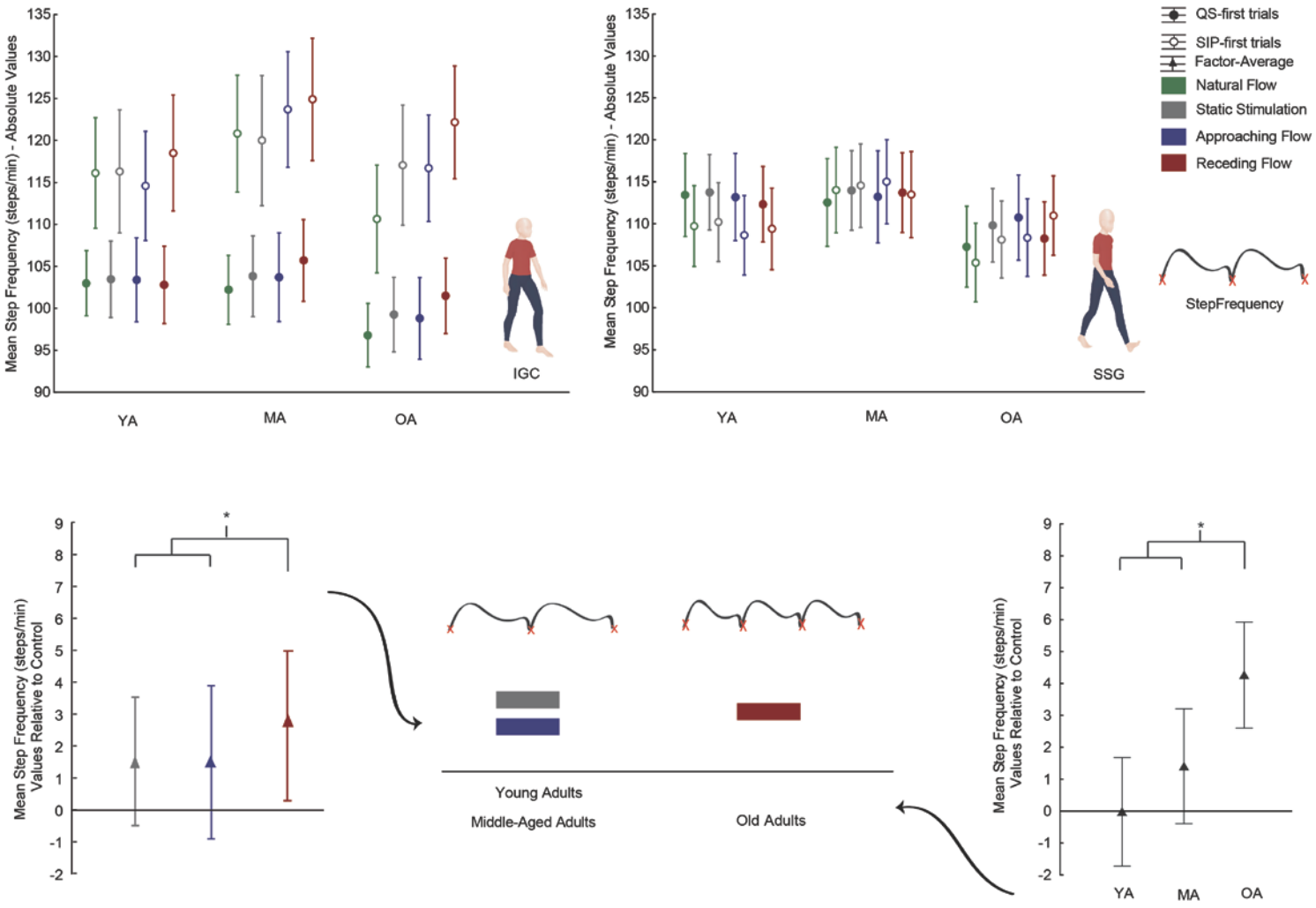

Figure IV.6 Top: Absolute values of mean step frequency across visual stimulation conditions for both trial types in each age group during the initial gait cycle (left) and steady state gait (right). Bottom: Values relative to the control condition revealing the main effect of visual stimulation and of age group illustrated between the graphs; left: imposed visual stimulation condition means pooled across age groups, gait cycles and initial postural conditions; right: age group means pooled across visual stimulation conditions, initial postural conditions and gait cycles. Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

IV.3.2.2 *Head and trunk mean pitch orientation*

Mean head and trunk pitch orientations during the control condition are also presented in Figure IV.3. For head pitch orientation, a main age group effect ($F(2, 53)=9.57$, $\eta^2= 0.27$, $p=0.000$) revealed a mean downward head pitch in old adults compared to young and middle-aged adults ($p<0.05$). The old adults held their heads about 5° lower than the younger participants with a mean of 83.34°. Middle-aged adults held their head up the highest with a mean of 89.14° and young adults had a mean of 86.78°. Moreover a gait cycle vs. age group interaction effect ($F(2, 53)=3.97$, $\eta^2=0.13$, $p=0.025$) revealed that old adults had a significantly lower mean head pitch orientation during the initial gait cycle compared to steady state gait while this was not observed for the other age groups ($p<0.05$) as may be seen in Figure IV.7. It is possible that for gait initiation old adults were more compelled to lower their gaze along with their head despite the instruction to look straight ahead in order to ensure a safe transition from quiet standing or stepping in place to walking forwards. Taking the mean trunk pitch orientation next, we observed a main effect of age group close to significance ($p=0.051$). Young adults leaned further forwards than the middle-aged and old adults with a mean pitch angle of 83.19° compared to 84.33° and 84.27° respectively.

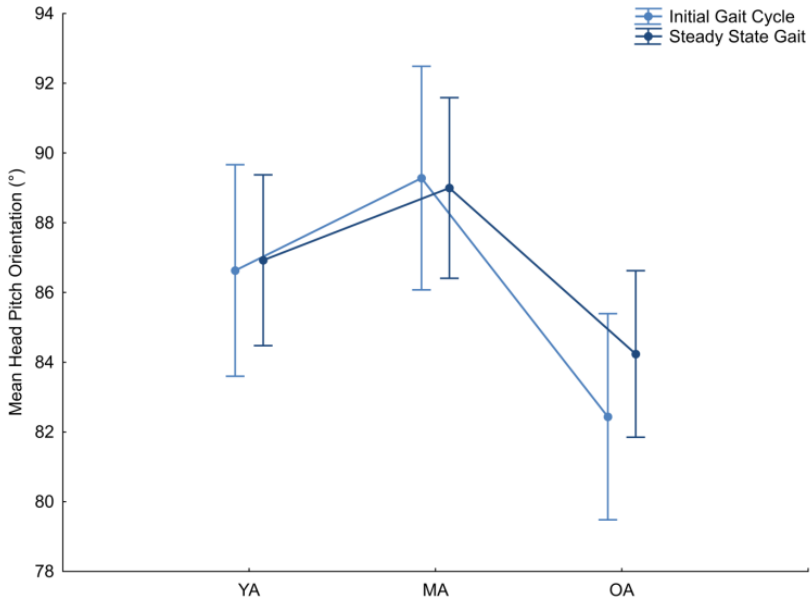

Figure IV.7 Baseline mean head pitch orientation for each age group during the initial gait cycle and steady state gait. Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults.

Examining next the head pitch orientation data relative to the control condition under conditions of imposed visual stimulation a main effect of optic flow was observed ($F(2, 106)=29.70$, $\eta^2=0.36$, $p=0.000$) whereby the

mean head pitch under approaching and receding flows was further back than during the static stimulation condition ($p<0.05$). While a gait cycle vs. visual stimulation interaction effect ($F(2, 106)=8.66$, $\eta^2=0.14$, $p=0.000$) revealed that relative mean head pitch values were greater during the initial gait cycle compared to steady state gait under the optic flow conditions ($p<0.05$), a gait cycle vs. visual stimulation vs. age group interaction effect ($F(4, 106)=2.65$, $\eta^2=0.09$, $p=0.037$) indicated that this difference was significant only for the old adult group ($p<0.05$). This is linked to the fact that old adults held their head lower during the initial gait cycle compared to steady state gait during the control condition. Figure IV.8 illustrates the mean head pitch orientation results and Figure IV.9 illustrates those of the mean trunk pitch orientation. A main effect of visual stimulation was also found for the relative trunk pitch orientation values ($F(2, 106)=12.49$, $\eta^2=0.19$, $p=0.000$). Not following the observation at the head level, the trunk moved further back only under approaching flow compared to both static stimulation and receding flow ($p<0.05$), we therefore observe a directional effect of optic flow. Interestingly, a visual stimulation vs. age group interaction effect ($F(4, 106)=2.77$, $\eta^2=0.10$, $p=0.031$) revealed that this was only the case for the old adult group ($p<0.05$).

IV.3.2.3 ***Head and trunk stability***

1) Oscillation amplitudes

Head and trunk oscillation amplitudes during the control condition in all three planes for each age group are presented in Figure IV.10. We found that head oscillation amplitudes among old adults were slightly larger in pitch and slightly smaller in yaw compared to the younger participants, however there were no significant age group effects. An age group difference was found only for the amplitude of head oscillations in roll ($F(2, 53)=4.36$, $\eta^2=0.14$, $p=0.017$), whereby old adults had significantly lower oscillation amplitudes than the young ($p<0.05$).

For the trunk oscillation amplitudes in all three planes were smaller for old adults compared to the younger participants. Age group effect found for the trunk oscillation amplitudes in pitch ($F(2, 50)=5.59$, $\eta^2=0.18$, $p=0.006$) and yaw ($F(2, 50)=8,4223$, $\eta^2=0.25$, $p=0.001$) revealed that these were smaller for old compared to young adults ($p<0.05$). While an age group effect for trunk oscillation amplitudes in roll ($F(2, 50)=10,936$, $\eta^2=0.30$, $p=0.000$) showed significantly smaller trunk oscillation amplitudes in old adults compared to both other age groups ($p<0.05$).

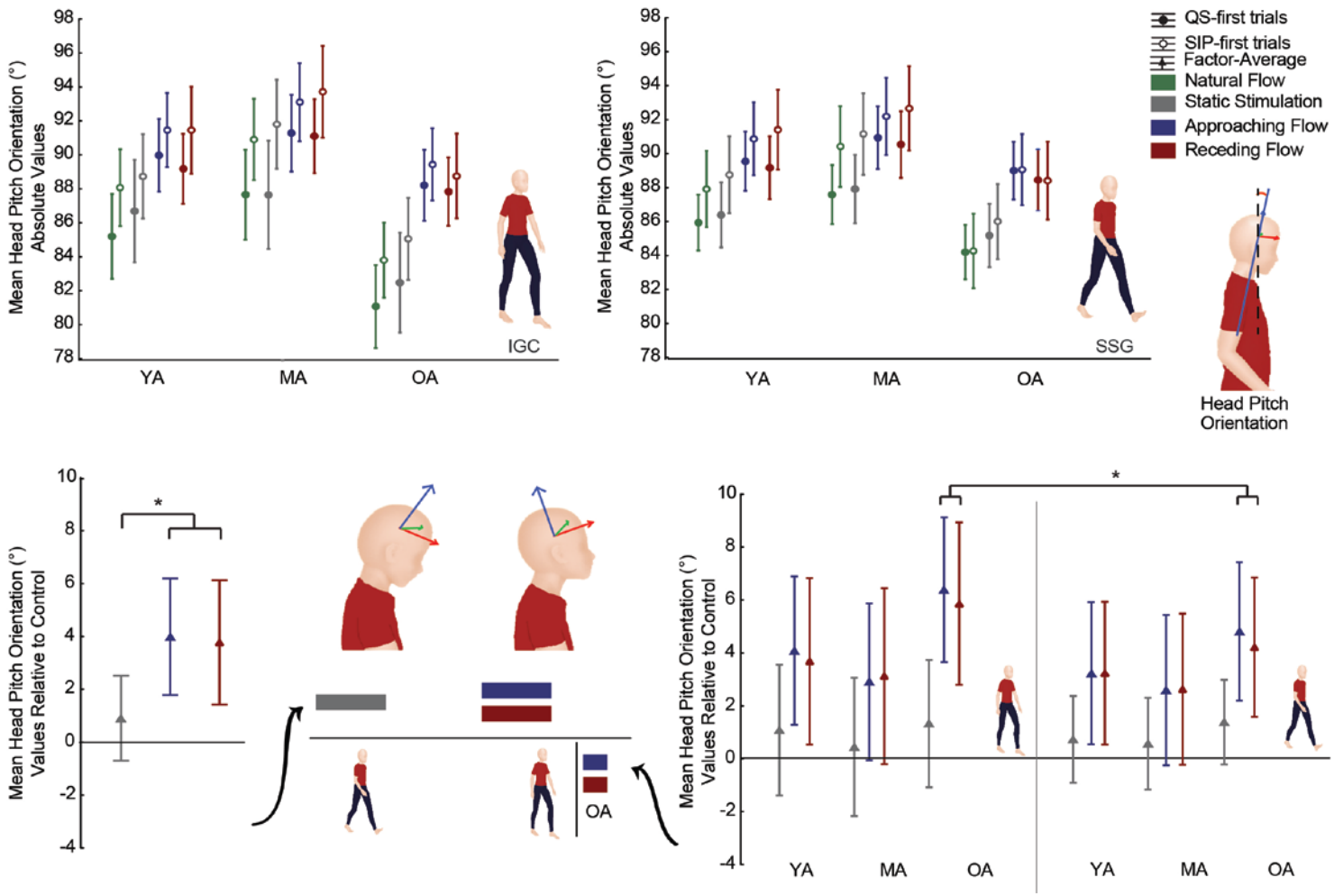

Figure IV.8 Top: Absolute values of mean head pitch orientation across visual stimulation conditions for both trial types in each age group during the initial gait cycle (left) and steady state gait (right). Bottom: Values relative to the control condition revealing the main effect of visual stimulation and interaction effect with age group and gait cycle illustrated between the graphs; left: mean values for each visual stimulation condition pooled across age groups, initial postural condition and gait cycles; right: age group means pooled across initial postural conditions for each visual stimulation condition during the initial gait cycle (left) and steady state gait (right). Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

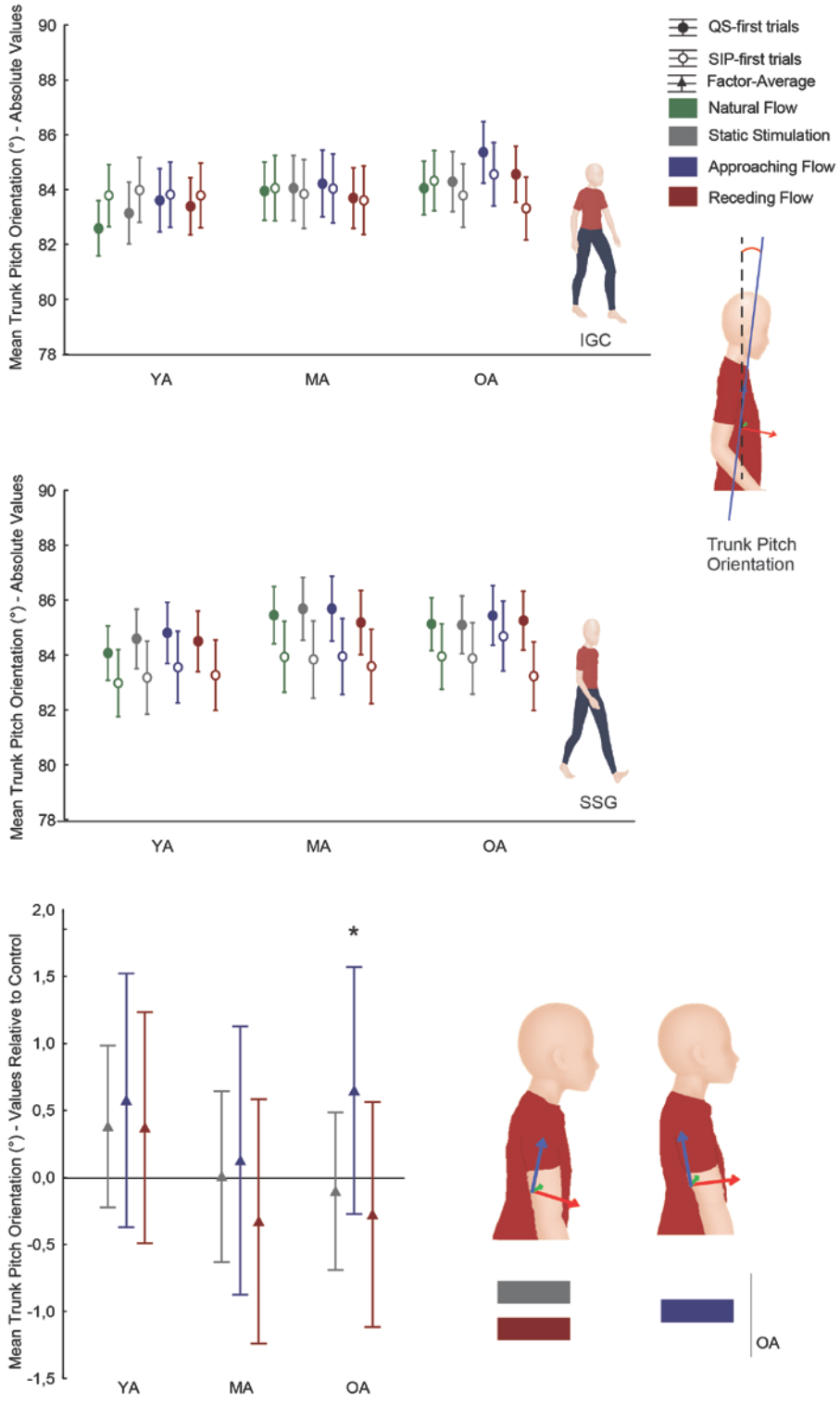

Figure IV.9 Top: Absolute values of mean trunk pitch orientation across visual stimulation conditions for both trial types in each age group during the initial gait cycle (left) and steady state gait (right). Bottom: Values relative to the control condition for each age group under the imposed visual stimulation condition pooled across gait cycles and initial postural condition revealing the visual stimulation interaction effect with age group illustrated on the right. Error bars indicate 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

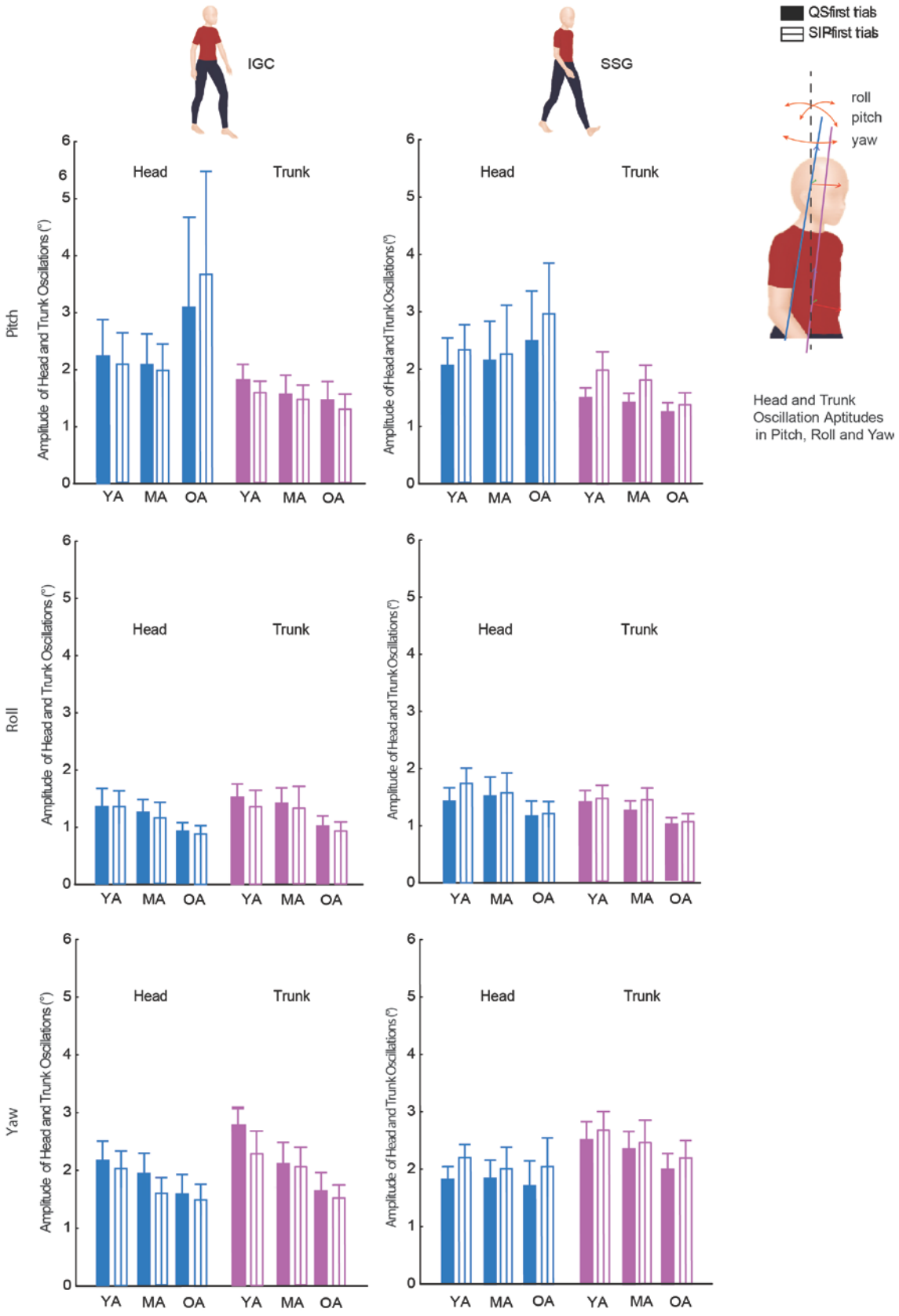

Figure IV.10 Baseline values for head and trunk oscillation amplitudes in pitch, roll and yaw for each age group during the initial gait cycle (left) and steady state gait (right) for QS-first and SIP-first trials. Error bars indicate upper limit of 95% confidence intervals. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

Considering next the values of head and trunk oscillation amplitudes relative to the control condition under conditions of imposed visual stimulation, we found that the stimuli influenced head and trunk oscillation amplitudes in pitch only, i.e. in the plane of stimulation as shown in Figures IV.11 and IV.12. The amplitude of head oscillations in pitch was reduced under approaching and receding flow compared to static stimulation ($p<0.05$) as indicated by a main visual stimulation effect ($F(2, 106)=13.28$, $\eta^2=0.20$, $p=0.000$). As may be observed in Figure IV.11 as well, the amplitudes were lower compared to during the control under all three stimulation conditions. Interestingly, a gait cycle vs. visual stimulation interaction effect ($F(2, 106)=3.08$, $\eta^2=0.06$, $p=0.050$) revealed that under both optic flow conditions, head pitch oscillation amplitudes were smaller during the initial gait cycle compared to steady state gait ($p<0.05$). It would appear therefore that the optic flow stimuli led to a better head stabilisation in the initial gait cycle which requires a greater need for postural balance compared to during steady state gait, as this difference between cycles was not observed under static stimulation. In addition, amplitudes under both optic flow conditions were smaller than under the static stimulation condition during the initial gait cycle while during steady state gait the difference lay only between receding flow and static stimulation ($p<0.05$).

For the trunk oscillation amplitudes in pitch we found an initial postural condition vs. gait cycle vs. visual stimulation interaction effect ($F(2, 106)=5.46$, $\eta^2=0.09$, $p=0.006$). Similarly to the effect observed on the amplitude of head oscillations in pitch, Tukey's HSD revealed that trunk pitch oscillation amplitudes were smaller during the initial gait cycle compared to steady state gait under both optic flow conditions in QS-first trials and under receding flow in SIP-first trials ($p<0.05$), indicating again the optic flow stimulus as a facilitator for stabilisation during the initial gait cycle. Contrary to the amplitudes of head oscillations in pitch, however, those of the trunk did not appear to reduce globally under optic flow conditions compared to static stimulation. The *post hoc* test revealed a directional effect of optic flow was found however during steady state gait of SIP-first trials, where amplitudes were on average greater under receding flow compared to approaching ($p<0.05$) as may be seen in Figure IV.12.

2) Head stabilisation strategies across visual stimulation conditions and motor tasks

Finally, we examined our participants' head stabilisation strategies by looking at the head-trunk anchoring index (AI) in pitch and in roll both during walking and the postural task on the force plate preceding each walking trial. Visual stimulation and age group differences were examined with repeated measures ANOVAs while stabilisation strategy was qualified with t-tests comparing AI values to zero. Bonferroni corrections were applied to the latter to account for the multiple comparisons with significance level being thus set to 0.0125, i.e. 0.05/the 4 visual conditions. As the variability associated with quiet standing and stepping in place is quite different between the two tasks, a visual stimulation (4) x age group (3) repeated measures ANOVA was performed for QS and SIP data separately. For the walking data an initial postural condition

(2) x gait cycle (2) x visual stimulation (4) x age group (3) repeated measures ANOVA was performed in order to consider possible effects of the preceding postural task and gait cycle as well. The AI in pitch and roll were examined separately.

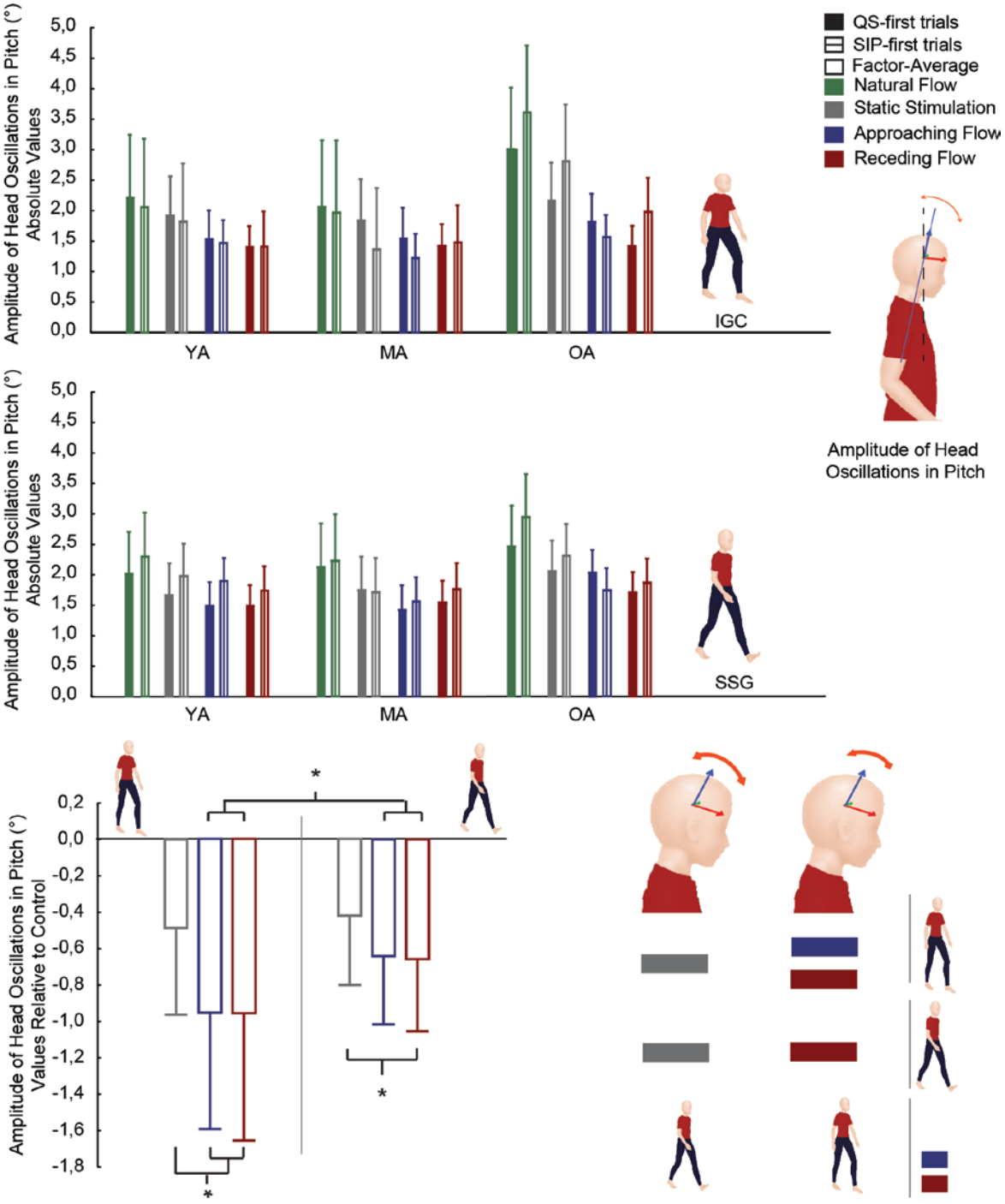

Figure IV.11 Top: Absolute values of head oscillation amplitudes in pitch across visual stimulation conditions for both trial types in each age group during the initial gait cycle (left) and steady state gait (right). Bottom: Values relative to the control condition (left) revealing the interaction effect of visual stimulation with gait cycle illustrated on the right. Error bars indicate 95% confidence interval limits. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

During quiet standing, no effects of age group or visual stimulation were found for the AI in either pitch or roll. During quiet standing all participants showed an *en bloc* stabilisation strategy with the head rigid on the trunk under all visual stimulation conditions both in pitch and in roll as may be seen in Figure IV.15. While stepping in place, however, main effects of age group and visual stimulation were found for the AI in both pitch (age group: $F(2, 53)=13.73$, $\eta^2=0.34$, $p=0.000$; visual stimulation: $F(3, 159)=3.48$, $\eta^2=0.06$, $p=0.017$) and roll (age group: $F(2, 53)=3.93$, $\eta^2=0.13$, $p=0.026$; visual stimulation: $F(3, 159)=4.10$, $\eta^2=0.07$, $p=0.008$) as may be seen in Figures IV.13 and IV.14 respectively. Tukey's HSD tests revealed that the average AI value of old adults in pitch was significantly lower than that of middle-aged and young adults ($p<0.05$) and that the pitch AI was greater under approaching flow compared to the control and static stimulation conditions ($p<0.05$). For the AI in roll, the post hoc tests revealed that old adults had significantly lower AI values than middle-aged adults ($p<0.05$) and that mean AI values were greater under static stimulation and approaching flow compared to the control condition ($p<0.05$).

Next, we considered our participants' head stabilisation strategies while walking. An age group effect ($F(2, 53)=3.57$, $\eta^2=0.12$, $p=0.035$) was found only for the AI in pitch as illustrated in Figure IV.13. The old adults, on average, had significantly lower AI values than the middle-aged adults ($p<0.05$). A gait cycle vs. age group interaction effect ($F(2, 53)=5,23$, $\eta^2=0.17$, $p=0.008$) however, revealed that during the initial gait cycle old adults had significantly lower AI values than both the young and middle-aged adults, while no age differences were observed during steady state gait ($p<0.05$). Main effects of visual stimulation were found for both the AI in pitch ($F(3, 159)=6.50$, $\eta^2=0.11$, $p=0.000$) and in roll ($F(3, 159)=7.25$, $\eta^2=0.12$, $p=0.000$). Tukey's HSD indicated that AI values in pitch were significantly greater under both approaching and receding flows compared to the control condition ($p<0.05$). For the AI in roll, values were greater under all three imposed visual stimulation conditions compared to the control condition ($p<0.05$) as may be seen in Figure IV.14.

To summarise, the head stabilisation strategies employed by age group and task in both rotation planes are illustrated in Figure IV.15 under each visual stimulation condition. The percentages indicated are based on the results of the t-test analysis performed for the anchoring indices in pitch and roll. The results of the t-tests are presented in Tables VI.3 and VI.4 (c.f. Appendix 2, pp 139, 140) for each age group under all visual stimulation conditions and for all tasks for the AI in pitch and in roll, respectively. In Figure IV.15 below, we observe that old adults use the head stabilisation in space strategy the least compared to the other age groups and in particular under the control condition. We also observe an improvement towards head stabilisation in space under conditions of imposed visual stimulation compared to the control condition, except for the middle-aged adults who frequently use the head stabilisation in space strategy during natural visual stimulation condition as well. Considering the influence of the task irrespective of age group, we see that head stabilisation in space was observed more frequently in the walking and stepping in place tasks compared to quiet standing. In addition, although significant increases were found for the AI values between natural flow and the imposed visual stimulation conditions as we saw above, in terms of strategy these

reflect, the imposed visual stimulation led to more frequent head stabilisation in space, compared to the control condition only for the walking tasks.

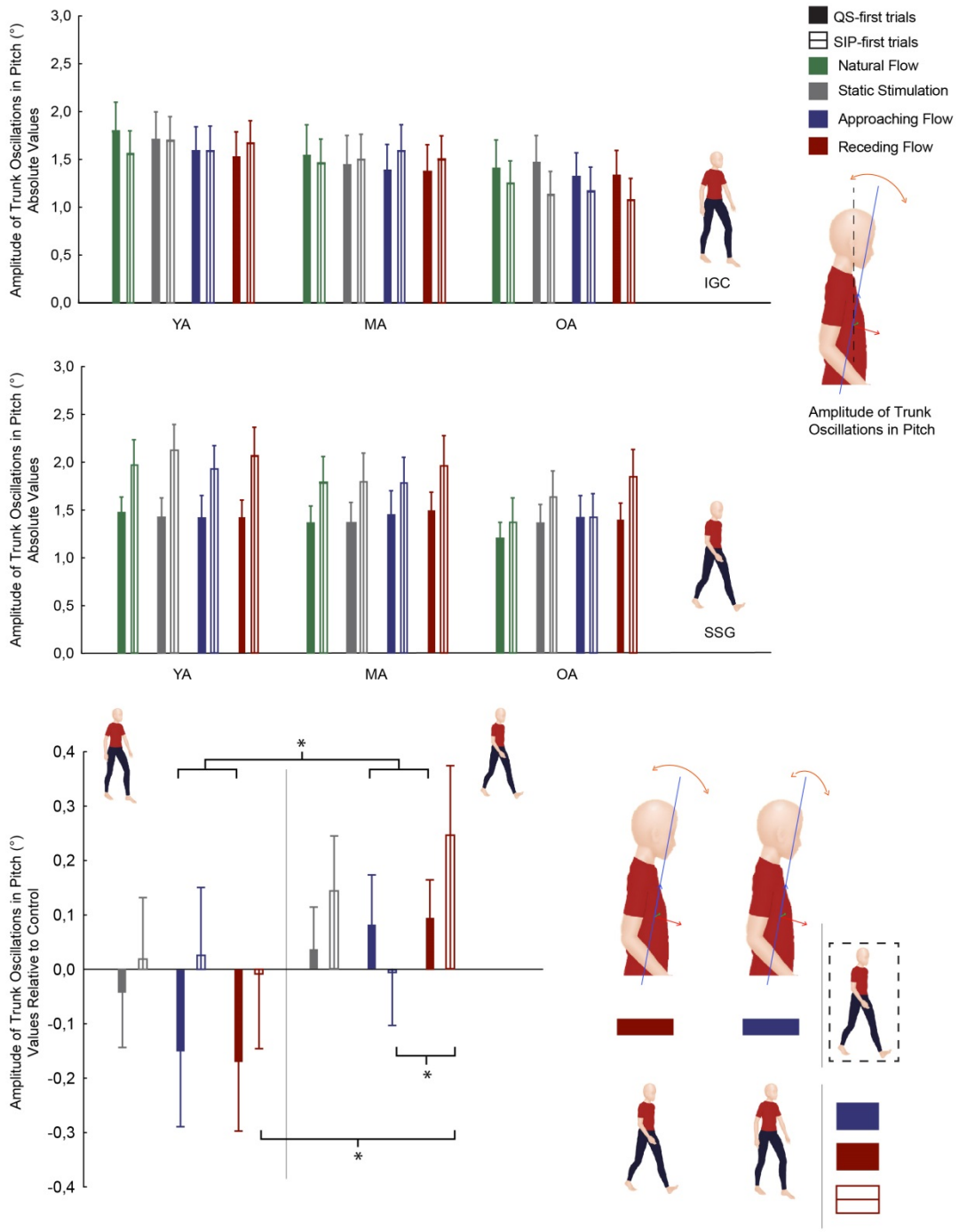

Figure IV.12 Top: Absolute values of trunk oscillation amplitudes in pitch across visual stimulation conditions for both trial types in each age group during the initial gait cycle (left) and steady state gait (right). Bottom: Values relative to the control condition (left) revealing the interaction effect of visual stimulation with age group and gait cycle illustrated on the right. Error bars indicate 95% confidence interval limits. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

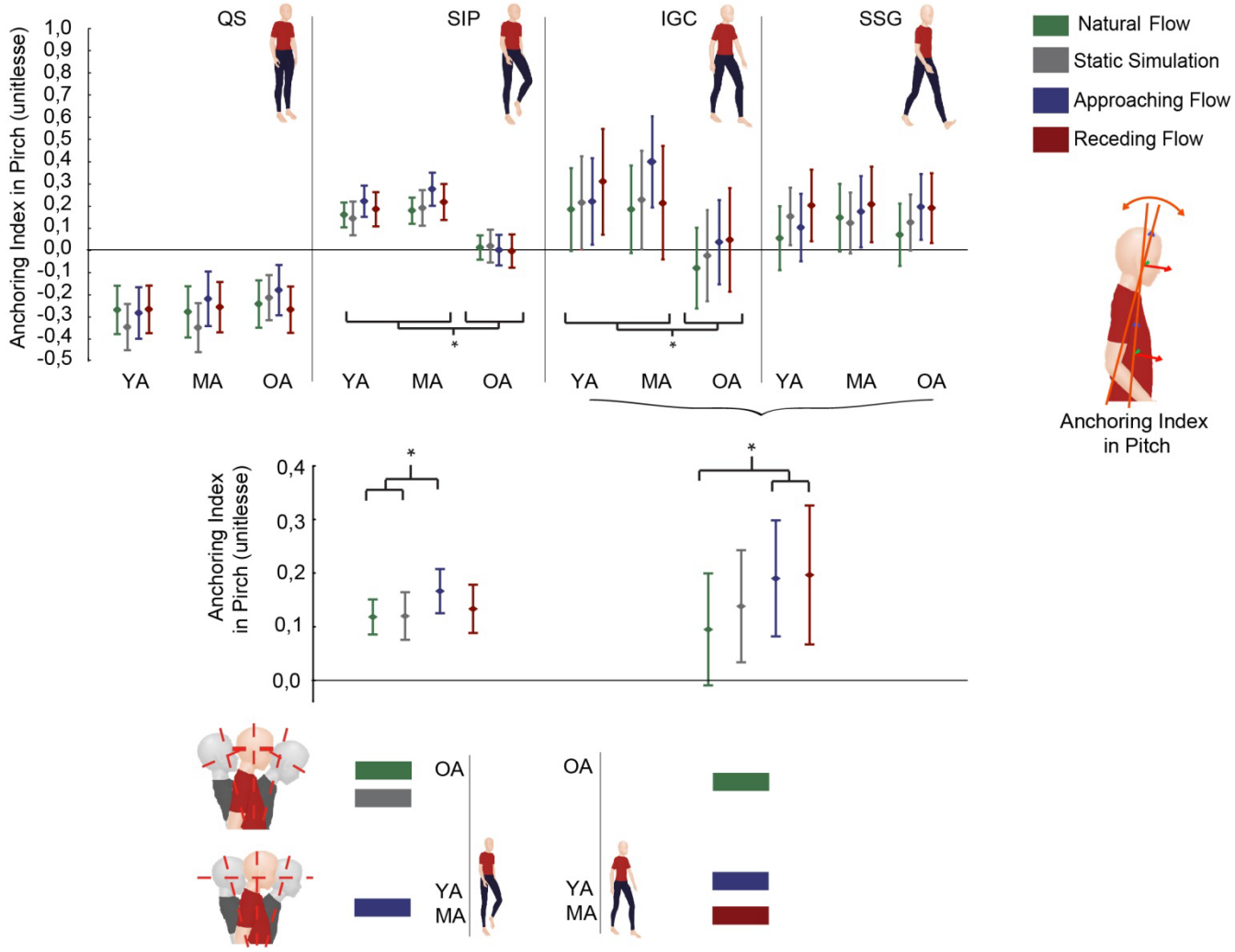

Figure IV.13 Top: AI values in pitch across visual stimulation conditions in each age group from quiet standing (far left) to steady state gait (far right). For the walking data, values indicated are means of QS-first and SIP-first trials. Centre: Main effects of visual stimulation presented for stepping in place (left) and walking (right), means are presented averaged across age groups and, for walking, gait cycles and initial postural conditions. Bottom: Age and visual stimulation effects illustrated. Error bars indicate 95% confidence interval limits. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

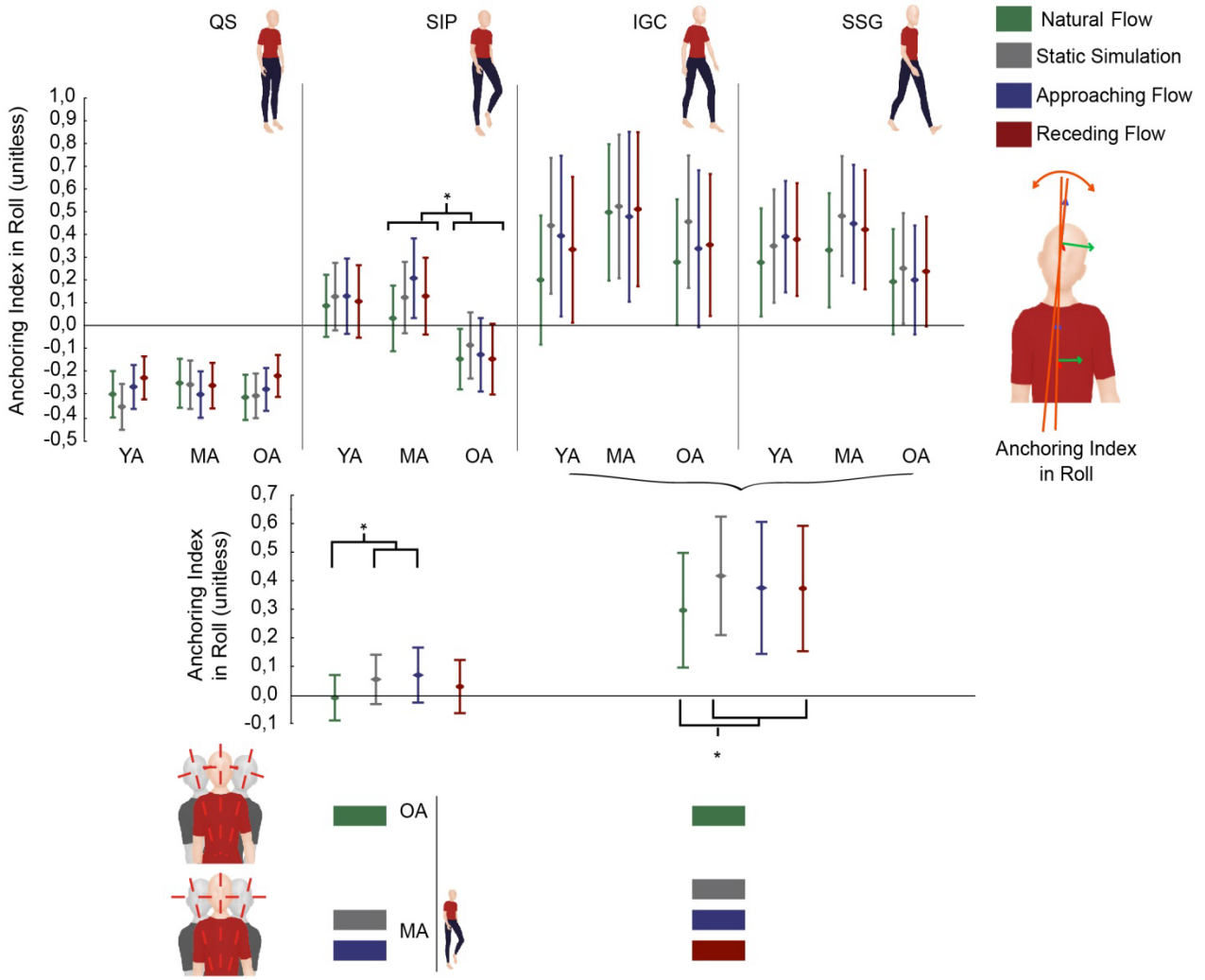

Figure IV.14 Top: AI values in roll across visual stimulation conditions in each age group from quiet standing (far left) to steady state gait (far right). For the walking data, values indicated are means of QS-first and SIP-first trials. Centre: Main effects of visual stimulation presented for stepping in place (left) and walking (right), means are presented, averaged across age groups and, for walking, gait cycles and initial postural conditions. Bottom: Age and visual stimulation effects illustrated. Error bars indicate 95% confidence interval limits. YA: young adults; MA: middle-aged adults; OA: old adults; IGC: initial gait cycle; SSG: steady state gait.

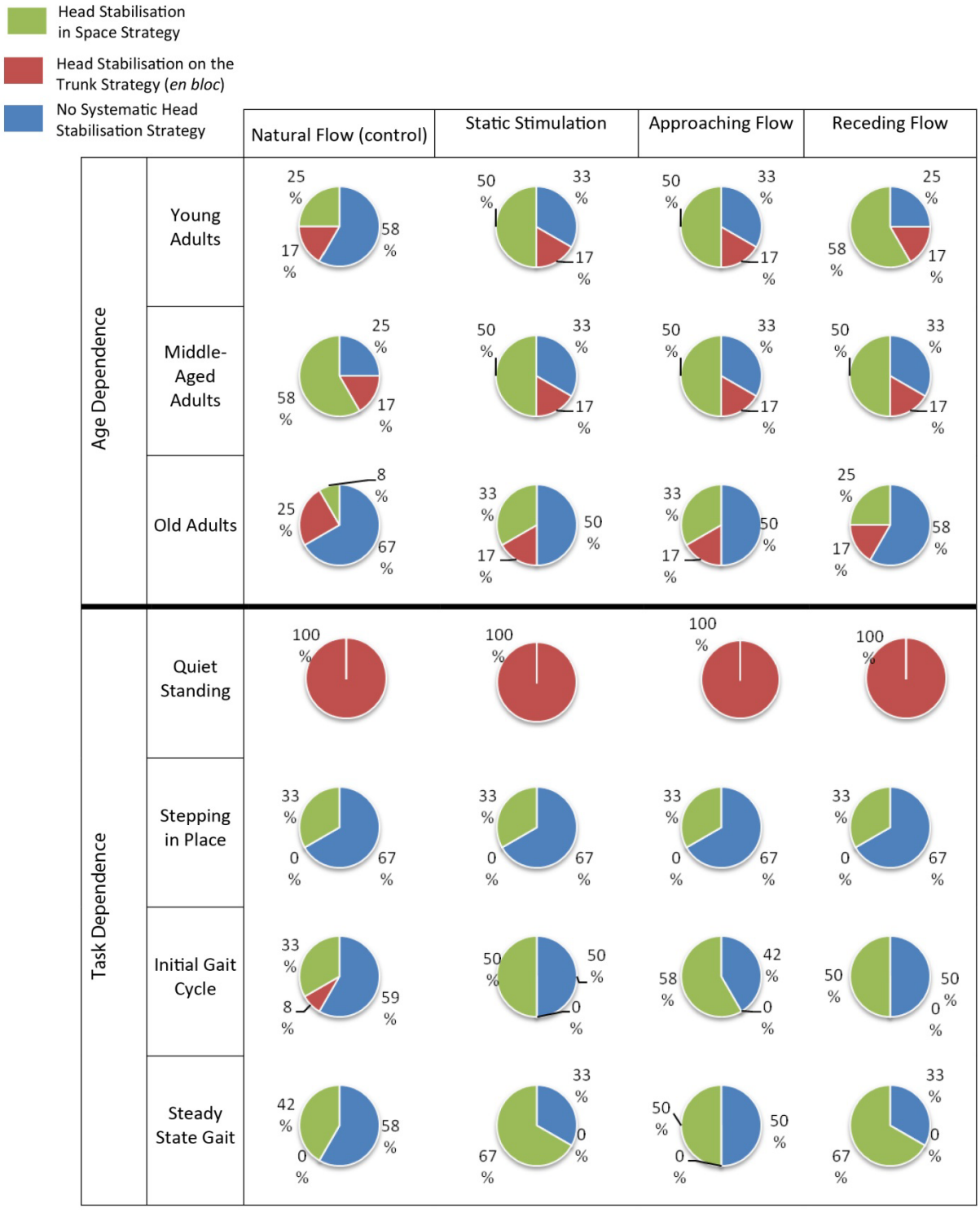

Figure IV.15 Illustration summarizing the age (top) and task (bottom) dependence of the head stabilisation strategy employed (for both pitch and roll rotations) based on the results of the t-test analysis for each visual stimulation condition.

IV.4 Discussion

Several interesting results have emerged through this experiment which may provide insight on how old adults use visual cues while walking, the effect of providing artificial optic flow as a visual stimulus and the appropriate design of studies aiming to identify differential contributions of visual and egocentric cues to the control of walking.

IV.4.1 Interpreting old adults' behaviour with respect to reliance on the visual FoR

The following interesting observations were found to reveal differences between our age groups:

- Lower head pitch of old adults while walking under natural flow compared to younger participants
- Backward mean trunk pitch under approaching flow observed only in old adults
- Reduced ability of old adults to stabilise the head in space compared to the young and middle-aged
    - in pitch during stepping in place and the initial gait cycle
    - in roll during stepping in place only
- Increase of step frequency under conditions of imposed visual stimulation in old adults compared to the other two groups

While age group differences on locomotor parameters are often reported, differences in head pitch orientation have received less attention. Moreover, the only study, to our knowledge, to examine head orientation in the frontal plane while walking – excluding studies on kyphosis – actually revealed a greater backward pitch among old adults compared to young adults (Hirasaki et al., 1993). We found that old adults held their heads comparatively lower with respect to the younger participants while walking under natural flow, and that this difference was even greater during the initial gait cycle compared to steady state gait. Hirasaki and colleagues speculated that the backward head pitch of old adults may be associated with an age-related vestibular deficit given that tilting the head backwards reduces vestibular sensitivity (Brandt et al., 1981; Della Santina et al., 2005; Schubert et al., 2004). However, we may consider an alternative interpretation. Our hypothesis would be that exactly because of age-related degradations to the vestibular system (Sloane et al., 1989), old adults may compensate when walking by leaning the head further forwards to maximise vestibular sensitivity, particularly in the more balance-threatening situation of gait initiation. Moreover, tilting the head downward maximises the acquisition of ground visual information as well. The

fact that despite our instructions to look straight ahead old adults reduced their head pitch orientation when walking (but not during quiet standing or stepping in place) agrees with findings revealing that old adults on average have a lowered gaze and rely more on their central vision when walking compared to young adults (Itoh & Fukuda, 2002) and maintain a lowered gaze for longer than young adults when negotiating stairs (Zietz & Hollands, 2009) and obstacles (Paquette & Vallis, 2010). It is possible therefore that old adults' greater reliance on the visual FoR and possibly associated vestibular impairments (Manchester et al., 1989), led them to reduce their head pitch orientation in order to acquire visual information on a more central region of their retina and to maximise vestibular sensitivity. This would also conform to our thesis, in agreement with previous studies (Boisgontier, Olivier, Chenu, & Nougier, 2012; Shaffer & Harrison, 2007), that somatosensory cues are noisier/more difficult to exploit with age. The lowered head pitch orientation of old adults under natural flow may constitute a compensations strategy given that self-motion information from the somatosensory system is not as salient.

The need to maximise visual and vestibular cue saliency, due to these systems' aging, may also explain the lower AI values found for old adults compared to the young and middle-aged adults. A key finding in this experiment was the loss of systematic head stabilisation in space for old adults, revealed via the head-trunk anchoring index. It has been suggested that a more rigid head stabilisation strategy may serve to reduce the processing burden associated with complex somatosensory relationships involving multiple degrees of freedom and accentuate visual feedback in order to improve the visual contribution to postural control (Isableu et al., 2010). This could also explain the smaller head and trunk oscillation amplitudes in old adults compared to the younger participants during the control condition. Although reducing segmental oscillation amplitudes is an indication of improved stability (Pozzo et al., 1990), in this context it may signify an 'over-control' in old adults, taken together with their less articulated head-trunk stabilisation strategy and lowered head pitch orientation, in order to maintain stability on the one hand and enhance the salience of sensory cues on the other. Furthermore, if we consider that old adults may have a relatively more bottom up stabilisation strategy this would explain why modulations of the trunk pitch orientation under visual stimulation occurred only for this age group. A directional effect of ground optic flow was found on mean trunk pitch orientation while walking among the old adults while visual stimulation differences were not significant for the other age groups. If indeed old adults rely on the visual FoR to a greater degree for spatial orientation, this may extend to their postural control and be revealed in the orientation of their body in order to align it with the visual direction of motion, in this case the trunk. Indeed it has been shown that in old adults, head stabilisation in space is not only impaired, but also reliant on the sensory signals arising from the trunk (Keshner, 2004). The question however arises as to why we did not observe this age group vs. visual stimulation interaction on the mean trunk pitch orientation during the postural tasks described in Chapter 3. During quiet standing and stepping in place (though for the latter only a trend was found, $p=0.056$) the same directional effect of ground optic flow was found on mean trunk pitch orientation, though this was not particular to specific age groups. It is possible that the visual-egocentric incongruence during quiet standing and the greater susceptibility to ground optic flow during stepping in place, given the intermittent podal

contact with the ground surface, led all our participants to behave in a similar manner. During walking on the other hand, where optic flow is a visual affordance and therefore the visual-egocentric discordance is reduced compared to the postural tasks, the same directional effect on the trunk pitch orientation appeared to manifest only in the more visual field dependent participants, the older adults.

Finally, while all participants increased their stepping frequency under receding optic flow, a simple age group effect revealed that the increase in stepping frequency under imposed visual stimulation was more prominent in the old adults. This may also be considered a sign of greater reliance on the visual FoR since these participants responded to the augmented visual stimuli with an increase in stepping frequency and no concurrent augmentations of step length or walking speed (indeed, depending on the optic flow direction either or both of these locomotor parameters were reduced). This may be considered an adaptation strategy, as was observed during stepping in place in the previous chapter, because it allows for more frequent phases of double limb support thus limiting postural instability. It should be noted that old adults' stepping frequency during the control condition was lower than that of the younger participants, however it is the relative increase that reveals their differential response compared to the other age groups.

IV.4.2 Optic flow influence on head stability

A very interesting finding in this experiment was the influence of ground optic flow on head pitch oscillation amplitudes and head stabilisation strategy. Based on reports in the literature that a) individuals more reliant on the visual reference frame such as children and Parkinson's disease patients show an *en bloc* head stabilisation on the trunk when walking and b) visual field dependent individuals show an *en bloc* strategy under visual-egocentric sensory discordance in postural tasks we hypothesised that old adults would show a more rigid head-trunk stabilisation behaviour under conditions of optic flow given the potentially more destabilising visual-egocentric sensory discordance for these participants. Contrary to our hypothesis, our old adults, also being the more reliant on the visual FoR participants did not adopt a more rigid head stabilisation strategy under conditions of imposed visual stimulation. Although age differences were found indicating reduced head stabilisation in space in old adults compared to the younger participants, all participants showed increased values of pitch and roll anchoring indices under conditions of visual stimulation. Moreover, head oscillation amplitudes in pitch were reduced under both optic flow conditions as well. These results lead us to consider that perhaps we should not regard our stimulus as a perturbation causing sensory conflict, but rather as an enhancement of visual self-motion information. Research on head stabilisation while walking with altered optic flow is limited. Studies examining head stabilisation in children walking when peripheral or dynamic visual cues were limited however showed little effect on the head stabilisation if not an improvement towards head stabilisation in space for the more visually reliant children (Assaiante &

Amblard, 1993). Enhancing optic flow on the one hand by means of stripes on the ground has revealed an improvement in the gait of Parkinson's disease patients (Azulay et al., 1999) however it did not seem to affect their head stabilisation strategy (Azulay, 1998). In our experiments however, both head and trunk oscillation amplitudes in pitch were further reduced under conditions of optic flow during the initial gait cycle compared to steady state gait, the former being a more threatening task for postural stability. It may be, therefore, that by providing ground optic flow which accentuated the perception of our participants' self-motion, the head stabilisation improved, as is the case when moving faster. This is further supported by considering also the task dependence of head stabilisation strategies adopted as represented in Figure IV.15 whereby the visual stimuli lead to the more frequent adoption of the head stabilisation in space during walking but not while stepping in place.

The non-directionality of the optic flow effect on head stabilisation strategy, head oscillation amplitude in pitch and mean head pitch orientation raises the question of whether the backward head tilt observed under conditions of ground optic flow is associated with the improved head stability under these conditions. If we consider that our optic flow cues were in fact affordance enhancements rather than visual perturbations, why would our participants – and old adults in particular, given their lower head pitch to begin with – tilt their head backwards to limit the visual stimulation they perceived? Perhaps our stimuli were salient enough to be perceived in our old adults' peripheral vision and not require fovealisation as during the natural flow condition. On the other hand if we consider once more the greater vestibular sensitivity at lower head pitch orientations, tilting the head back would be a means to limit visual-vestibular conflict and place greater reliance on the dynamic peripheral visual information, on which visual field dependent individuals rely more for postural control (Assaiante & Amblard, 1992; Azulay et al., 1999; Isableu et al., 2010; Isableu et al., 1998; Isableu et al., 2010).

An alternative proposition is that our optic flow stimuli were indeed sensory perturbations which would require an appropriate postural adaptation for better control. The adaptation therefore was transcribed in an improvement of head stabilisation in space, given that this is the most appropriate strategy in the control of dynamic equilibrium (Berthoz & Pozzo, 1988). Indeed this was observed in both children and adults in the aforementioned study when available visual cues were limited (Assaiante & Amblard, 1993) and even while walking on a narrow beam in darkness in adults. In this case we may re-interpret the backward head pitch reorientation observed under optic flow conditions as a means to reduce the area of the retina being stimulated and consequently reduce the perceived sensory conflict between visual and egocentric sensory information on self-motion. It would be interesting for future studies to examine this question, possibly by providing visual stimuli of varying ecological significance. If indeed our results under optic flow conditions reveal an adaptation to sensory perturbation, it would also be of interest to examine the preservation of such postural adaptation abilities in old adults by assessing the head stabilisation strategies adopted under varying conditions of dynamic equilibrium difficulty such as beam walking.

IV.4.3 Designing appropriate protocols to examine sensory contribution to locomotor control

The aim of this experiment was to identify an index of reliance on the visual FoR while walking. We hypothesised that old adults' greater visual field dependence would manifest as a more rigid head stabilisation strategy under conditions of ground optic flow and/or a greater modulation in the locomotor parameters as adaptation to the visual stimuli over the 30 s period on the force plate would be slower or non-existent in this group compared to the younger participants. Neither of these hypotheses proved valid, we therefore consider the limitations of our protocol as well as our rationale.

The difference in the effect of a visual stimulation between our walking participants and visual field dependent individuals during postural tasks (Isableu et al., 2003) could be related to the combination of the nature of the motor task and the visual stimulus: walking with enhanced ground optic flow. AI values in both pitch and roll were lower during the quiet standing task compared to during stepping in place and walking and significantly below zero, indicating an *en bloc* head stabilisation strategy. The act of walking, or similar as is the task of stepping in place, would thus allow for a head-trunk coordination behaviour such that the acquisition and processing of visual and vestibular sensory information is optimised. As discussed in the previous chapter as well, the ground optic flow provided was effectively an enhanced visual affordance associated to walking and not standing and, in the case of stepping in place and walking, it is perhaps not a visual perturbation. We may note that, contrary to during stepping in place or walking, the optic flow did not improve head stabilisation in space during quiet standing; however, it did not exacerbate the rigid behaviour either.

Considering next the modulations in the locomotor parameters, we found certain effects of visual stimulation on step length, walking speed and step frequency but observed no interactions with age. Moreover, examining Figures IV.4 and IV.5, we see that there is variability between our age groups and the simple visual stimulation effects may be due to averaging across age groups rather than an indication of similar behaviour between the three age groups. It is possible that the effects of the ground optic flow stimulus were predominantly observed during the postural tasks and an adaptation to the visual stimulus occurred by the time participants were to walk across the walkway. Indeed Schubert et al. (2005) found that adaptations occurred even for old adults over time, with a shift to downweight visual information when walking under conditions of modified optic flow. Although we considered that given the difference in motor tasks and shorter time-scale of the period on the force plate compared to the periods examined in the above study, old adults did not show differential behaviour except for stepping frequency as discussed further above.

An improvement to our protocol could be providing augmented sensory conflict via (greater) visual and somatosensory perturbations which would also be more threatening to postural stability as is classically done in studies examining sensory reweighting in postural tasks. For example, given that postural instability is

greater in the mediolateral direction when walking (O'Connor & Kuo, 2009) and countering anteroposterior perturbations such as ours is facilitated by the propulsive forces of forward motion, introducing mediolateral perturbations to optic flow stimuli may be more effective to dissociate participants' relative reliance on the visual FoR when walking. By applying enhanced mediolateral oscillations to the visual scene provided, Brady et al (2012) were able to identify a portion of their young adult participants as more reliant on the visual reference frame given that the oscillation frequency of their trunk matched that of the visual scene they observed as opposed to their stepping frequency, as was the case for the participants less reliant on the visual frame of reference. Moreover, these authors used a multi-sensory perturbation paradigm by also applying mechanical perturbations to the base supporting the treadmill employed. by Franz et al. (2015) also revealed a more important reliance on the visual FoR in old adults by observing differences in dynamic stability between these and younger participants when faced with mediolateral perturbations in an optic flow stimulus. A finer analysis could also prove more revelatory of individual differences, for example using dynamical metrics, this would entail a different conceptualisation of the experimental protocol as well in order to acquire the necessary parameters for analysis.

IV.5 Conclusion

In conclusion, this study revealed differential behaviour between old and younger participants, the influence of the visual stimulation on our participants' control of walking, however, was not always age-dependent. Old adults' trunk re-orientation under approaching flow and increase in stepping frequency under both optic flow conditions may indicate a greater sensitivity to the visual FoR on the one hand for body orientation and on the other for maintaining postural stability while walking. These participants' reduced head pitch orientation and reduced ability to stabilise their head in space under the control condition may also be indicative of behaviour in order to maximise the salience of the available visual cues, possibly associated with reduced vestibular function. In addition, we observed a general improvement of head stabilisation under conditions of imposed visual stimulation. The amplitude of head oscillations in pitch, i.e. in the plane of stimulation reduced under conditions of optic flow and particularly during the initial gait cycle while an improvement in head stabilisation in space was observed under all imposed visual stimulation conditions. Contrary to our expectations, the artificial enhancement of the optic flow generated with one's motion may thus facilitate head stabilisation.

V. *Chapter 5: General Discussion*

V.1 Introduction

In this final chapter introduction, we shall bring together our main experimental findings in order to provide a global view of our research with respect to visual field dependence across adulthood and its manifestation across our different sensorimotor tasks. We proceed to address one of our main research questions: is reliance on the visual FoR a preferred mode of spatial referencing in old adults or a consequence of age-related deficits? The subsequent sections of this chapter deal with emerging themes of our work, namely:

- the evolution of sensorimotor control across adulthood with respect to reliance on the visual FoR,
- the implications of reduced reliance on the egocentric FoR in old age,
  and
- considerations and perspectives on the assessment of sensory reweighting for sensorimotor control.

V.1.1 Manifestations of visual field dependence

V.1.1.1 *From perceptual to perceptivo-motor reliance on the visual FoR*

Greater visual field dependence among old adults was confirmed via three widely used assessments in our first study, namely, the rod and frame test (RFT), the rod and disc test (RDT) and the group embedded figures test (GEFT), in accordance with the literature (Kobayashi et al., 2002; Marendaz, 1984; Markus, 1971; Panek et al., 1978; Schwatz & Karp, 1967). Old adults made greater adjustment errors in their subjective vertical estimation when faced with a disorienting static (RFT) or dynamic (RDT) visual stimulus and were not able to find and trace as many embedded figures as younger adults on the GEFT. With these tasks, we were able to reveal old adults' greater susceptibility to a distracting visual context and, importantly, how this reliance on the visual frame of reference affects both spatial orientation and higher order cognitive processes. During the postural tasks, quiet standing and stepping in place, we found that old adults relied on the visual FoR, in this case ground optic flow, for their self-motion perception to a greater extent than

younger participants. This was revealed by greater values of the visual self-motion quotient under both optic flow directions which are associated with larger drift while stepping in place. The latter denotes a condition where the podal contact with the ground surface is intermittent, thus reducing the prominence of the ground as a mode of spatial referencing for body alignment, orientation and stabilisation. During quiet standing where the permanent podal contact with the ground surface allows an easier exploitation of the ground as a reference, old adults were also found to be 'pushed' further back under approaching flow compared to young adults. These findings agree with the greater sway amplitudes observed in old as compared to young adults under oscillating optic flow conditions (Borger et al., 1999; Sparto et al., 2006a). Moreover, old adults increased their stepping frequency during the SIP task under imposed visual stimulation conditions compared to young adults. This last finding was observed during the walking tasks as well. Increasing one's stepping frequency may be considered as an adaptation strategy to maintain equilibrium in our protocol. This is because when step length does not increase concurrently (as was the case in our study), increasing the stepping frequency offers a greater amount of double support phases which allows for better exploitation of the ground reference and limits lateral instability as well. Finally, we interpreted old adults' trunk backward reorientation in pitch under approaching flow and their reduced head pitch orientation and ability to stabilise the head in space under natural flow as manifestations of a greater reliance on the visual FoR. The trunk reorientation would indicate that the optic flow provided was used as a reference for body orientation, while under natural flow the downwards head pitch orientation and the less articulated head-trunk stabilisation strategy would indicate an adjustment in postural control to render available visual cues more salient (Isableu et al., 2010).

V.1.1.2 *Associated factors and behaviour*

A main association uncovered in our work is that of increased reliance on the visual FoR and reduced reliance on the egocentric FoR. This was revealed first on the subjective vertical estimation tasks. Participants most influenced by the tilted frame (RFT) or rotating disc (RDT) in the adjustment of the tilted rod to vertical were less influenced by body-based cues whilst tilted themselves (rod and body test, RBT) when adjusting the rod to vertical in the absence of orienting visual information (reduced Aubert effect). In the stepping in place task, this finding extended to participants' self-motion perception, with greater values of the visual self-motion quotient being positively correlated to drifting without visual stimulation (natural drift). Moreover, the fact alone that ground optic flow effects were greater when the podal contact with the ground was minimised by stepping in place and especially among old adults and that they drifted even in the absence of the optic flow stimuli, indicates that this population was more affected by the intermittence of somatosensory cues for self-motion perception with respect to the ground. Interestingly, while the visual self-motion quotient correlated positively with scores on the RFT and RDT and negatively with the RBT, the correlation between natural drift and RBT scores was very low, indicating perhaps a differential exploitation

of the egocentric frame of reference for spatial orientation and for self-motion perception. This will be discussed in more detail further below. We also found that reduced visual fixation stability was associated with greater reliance on the visual FoR on the one hand and reduced reliance on the egocentric FoR on the other for the subjective vertical estimation tasks. This finding supports our hypothesis that greater visual field dependence is linked to a reduced ability to exploit the egocentric FoR as the somatosensory extra-retinal signals arising from more variable fixation eye movements would contribute noise to the kinematic proprioceptive chain linking the eye to the foot (Roll & Roll, 1988; Kavounoudias, Gilhodes, Roll, & Roll, 1999; Roll et al., 1991). We further consider that our results support the hypothesis of greater visual field dependence being associated to a kind of neglect, to a certain degree, of somatosensory cues and associated modes of spatial referencing for spatial orientation and self-motion perception in old adults. With age, somatosensory inputs may be considered less reliable while central age-related deficits in higher-order processes lead to difficulty in integrating such signals and allocating attentional sensorimotor resources to non-visual frames of reference, which in turn upweights visual cues.

The increased reliance on the visual FoR observed in old adults was also associated with how visual cues are perceived and processed. Throughout this work, we have convergent evidence that older participants were unable to ignore the disorienting visual contextual information provided, whether this was in order to estimate the direction of gravity (RFT, RDT), identify hidden (GEFT) figures or their location (UFOV), control their stepping while stepping in place, or the orientation of their trunk while walking. The positive correlation between greater visual field dependence and longer processing times required to complete the UFOV 2 and 3 subtests indicates that the capacity to allocate and share visual attention resources as well as the location of the stimulus (centre vs. periphery) contribute to visual field dependence. Indeed both the reduced attentional capacities (Goodenough et al., 1987; Yan, 2010) and sensitivity to peripheral visual cues (Assaiante & Amblard, 1992; Assaiante & Amblard, 1993; Isableu et al., 1998; Isableu et al., 2010) associated with reliance on the visual FoR are supported by our findings. Moreover, during the postural and locomotor tasks the limited (5 m x 1 m) area and eccentric position of our optic flow stimuli, stimulating only the upper region of the retina, were sufficient to provoke translation and re-orientation responses among old and more visual field dependent adults. Considering these findings as well as the association found with greater visual fixation instability, we support the hypothesis that increased visual field dependence with age relates to both sensorimotor and cognitive decline.

V.1.2 Evolution through adulthood

Depending on the indicator of reliance on the visual FoR examined, distinct age group differences were observed. On the classic tests of visual field dependence, scores indicating greater reliance on the visual FoR increased from young to middle-aged to old adults. While old adults had significantly higher values on all

three tests compared to young and middle-aged adults, the latter also showed significantly higher scores than young adults for the GEFT and RDT, indicating thus a progressive but marked increase in visual field dependence throughout adulthood. Interestingly, the middle-aged adult group had the greatest inter-individual variability on the GEFT, i.e. the more cognitive test of visual field dependence. In addition, greater sensitivity to visual cues for self-motion perception was evident from middle-age. These participants drifted backward while stepping in place under approaching flow as did – though to a greater extent – old adults, whereas no significant effect of ground optic flow was found for the young adults. While walking on the other hand, we did not observe indications of greater reliance on the visual FoR among middle-aged adults. Reliance on the egocentric FoR for spatial orientation and self-motion declined from young to old adulthood. Although this reduction was associated with greater visual field dependence, the decline appears less progressive with age. The reduction in the exploitation of the egocentric FoR may occur in early old age rather than gradually throughout adulthood given that we found differences between old adults and the two younger groups and no statistical difference between young and middle-aged adults.

It appears therefore that the preference of one mode of spatial referencing over another throughout adulthood is manifested differently depending on the task. The greater visual field dependence of middle-aged and old adults found on the subjective vertical estimations and GEFT is revealed in self-motion perception during stepping in place. When walking, however, only old adults showed behaviour that may relate to a greater reliance on the visual FoR. Interestingly, when walking under natural flow, middle-aged adults actually had the highest head pitch orientation and a more frequent head stabilisation in space strategy compared to the other age groups. Contrary to old adults, this indicates that the middle-aged participants did not adjust their behaviour to maximise the salience of the available visual cues. It is possible that vestibular inputs are upweighted while walking, thus reducing middle-aged adults' reliance on the visual FoR. A study has indeed revealed a peak in the contribution of vestibular signals for postural control in middle-age (Faraldo-Garcia, Santos-Pérez, Crujeiras-Casais, Labella-Caballero, & Soto-Varela, 2012) which may explain our observations. In addition, when walking under conditions of optic flow, the middle-aged adults did not differ from young adults either in their step frequency or trunk pitch orientation, contrary to the old adults who modulated these parameters.

V.1.3 Reliance on the visual FoR in old age: vicariant choice or compensation of deficits?

A central question of this work was the significance of increased reliance on the visual FoR in old age. Is this a preferred mode of spatial referencing – a vicariant choice as in young adults – that occurs as an adaptation to the sensorimotor and cognitive changes that occur with age? Or is it, rather, a compensation for such

changes that may not necessarily constitute a functional operation? The age-related changes that also appear linked to reliance on the visual FoR are the increased noise associated with somatosensory signals, the reduced reweighting capacity and attentional resources of old adults. Relying on the visual FoR in the context of these age effects may thus be considered an optimisation strategy in order to exploit the sensory input considered most reliable (i.e. visual cues) and reduce the number of degrees of freedom associated with a given sensorimotor task. This is done by limiting the potentially destabilising effect of allocating attention to and having to process multiple sources of information (from different modalities or even within the visual modality, e.g. as seen with the reduced UFOV and lowered head pitch while walking). Indeed, stiffening strategies for postural stability have been associated with visual field dependence in children (Assaiante & Amblard, 1993), young adults (Isableu et al., 2010; Isableu et al., 2003) and Parkinson's disease patients (Mesure et al., 1999) in terms of segmental coordination or in terms of muscle co-contraction in old adults (Slaboda et al., 2011). However, regardless of the noise and cognitive load associated with processing somatosensory input (Boisgontier, Olivier, Chenu, & Nougier, 2012), visual cues may not always be reliable either due to the environment, or to age-related deficits in visual perception and processing. In such cases, reliance on the visual FoR no longer constitutes a vicariant choice (optimal or equal to other FoRs) but a rigid strategy or very strong prior.

In the context of greater age-related deficits which reduce adaptation and reweighting ability, processing and acuity of the sensory systems as well as brain mass and functional activation patterns, reliance on the visual FoR is exacerbated and no longer functional. There is great inter-individual variability in the degradation rate of the above systems and processes with age and the associated sensorimotor behaviour. We found greater variability among old adults on most of our measures as well. We propose therefore that in old age, reliance on the visual FoR increases as age-related deficits aggravate and this mode of spatial referencing becomes no longer functional given that the combination of such deficits and the negative implications of visual field dependence do not permit a meaningful exploitation of visual cues even when these are reliable or an appropriate shifting of reliance to another FoR when they are not. The associations we have found between greater visual field dependence and reduced exploitation of the egocentric FoR (for both spatial orientation and self-motion perception), parallel attentional visual processing ability and visual fixation stability corroborate this hypothesis and previous studies associating greater reliance on the visual FoR in old adults with sedentary lifestyle (Karp, 1967; Markus & Nielsen, 1973; Rotella & Bunker, 1978), falls (Barr et al., 2016; Lord & Webster, 1990), reduced adaptation and reweighting abilities (Berard et al., 2012; Eikema et al., 2013).

V.2 Sensory reweighting and sensorimotor control with age

We proceed next to consider how reliance on the visual FoR is involved in sensory reweighting for sensorimotor control across the human lifespan.

V.2.1 (Anti-) Parallels between development and aging

Our work has highlighted the greater contribution of visual cues in different tasks, supporting a wide range of literature emphasising the changes that occur with old age in sensory reweighting. It is worth noting the similarities in the mechanisms of sensory reweighting and control strategies between young children and old adults.

In agreement with previous studies, we found a greater contribution of visual cues for the construction of one's subjective vertical among old adults (Agathos et al., 2015; Eikema et al., 2012; Kobayashi et al., 2002; Marendaz, 1984; Panek et al., 1978; Schwatz & Karp, 1967; Slaboda et al., 2011) which has also been reported in children (Bagust et al., 2013; Haywood, Teeple, Givens, & Patterson, 1977; Witkin, Goodenough, & Karp, 1967). Moreover, we found an increase in visual field dependence from young to middle-aged to old adulthood (also reported in an earlier study (Panek et al., 1978)), analogous to the decrease observed from childhood to adolescence to adulthood (Bagust et al., 2013; Witkin et al., 1967).

Contrary to other studies (Borger et al., 1999; Franz et al., 2015; O'Connor et al., 2008; Wade et al., 1995), the analysis performed in our experiments did not reveal greater postural instability among old adults under conditions of modified visual input, i.e. incongruent ground optic flow. What our data have revealed however is a greater influence of the visual FoR, with respect to the ground surface, on postural control in old adults compared to the younger participants, and a reduced contribution of somatosensory inputs for the postural tasks in particular. A greater influence of ground optic flow on postural control has also been found in children compared to adults (Baumberger et al., 2004) and a reduced ability to exploit somatosensory cues under visual-somatosensory conflict (Sparto et al., 2006). When somatosensory input is modified on the other hand, reliance on the visual FoR has not been enough to fully compensate for the induced perturbation (Cuisinier, Olivier, Vaugoyeau, Nougier, & Assaiante, 2011); this indicated a reduced ability to appropriately reweight sensory information in children, similarly to the reweighting deficits reported in old age (Eikema et al., 2013) or young visual field dependent individuals (Isableu et al., 2011).

Finally, considering inter-segmental stabilisation, our study has revealed that old adults appear to lose the ability to systematically stabilise their head in space, which is considered to facilitate the integration of visual

cues (Assaiante & Amblard, 1995). It seems that a regression in head stabilisation occurs in old age, opposite to the maturation in the effective use of the head stabilisation in space strategy at around 7 years of age (Assaiante & Amblard, 1993). Indeed, while the head becomes progressively more independent from the trunk with age (Grasso, Assaiante, Prévost, & Berthoz, 1998) the opposite has been observed in old age (Keshner, 2004). Contrary to young children resorting to a stiffening strategy to reduce the number of degrees of freedom involved in postural control under more difficult equilibrium conditions (Assaiante & Amblard, 1993), old adults did not block the head on the trunk under conditions of optic flow. On the contrary, the AI actually increased towards more positive values although not always reaching significant difference from zero which would indicate a systematic head stabilisation in space strategy. If we consider optic flow stimuli as perturbations causing visual-egocentric incongruence, then we may suggest that old adults behaved similarly to the younger participants. The older participants responded to the perturbation by an adjustment in head and trunk coordination in order to improve their stability, the increase in stepping frequency was another indication of such adaptation. The difference between young children and old adults may therefore be due to the fact that old adults have a larger repertoire of sensorimotor experiences (priors or bases of knowledge) that would aid them to adopt the more appropriate head stabilisation strategy when most necessary, i.e. under sensory perturbation.

V.2.2 Transition in aging: behaviour of middle-aged adults

Research on middle-aged adults is sparse, very possibly due to the inter-individual differences within this population and the variability in the rate of decline of different cognitive processes (Hedden & Gabrieli, 2004) and sensorimotor systems (Lord & Ward, 1994). As we briefly noted further above, depending on the task examined, middle-aged adults appeared to behave similarly to young or to old adults or constitute a group significantly different from both others with an intermediate performance. This has already been reported in the control of balance, where the task conditions reveal differences in the decline of postural stability with age. While no differences have been found in postural sway between young and middle-aged adults during bipedal and monopedal stance with eyes open (Hurley et al., 1998), removing vision (Hurley et al., 1998) and concurrently altering somatosensory information either using a foam support surface (Abrahamova & Hlavacka, 2008; Choy, Brauer, & Nitz, 2003) or during monopedal stance (Choy et al., 2003; Hurley et al., 1998) increases sway in middle-aged adults revealing different sensitivities to sensory information for postural control compared to younger individuals. We see therefore that depending on the task and context, the sensory contributions and emergent behaviour follow transitions at different ages.

In our study middle-aged adults differed from the young adults with respect to the greater contribution of dynamic visual cues but not regarding their reliance on static, geometric visual cues in the construction of the

subjective vertical. Moreover the influence of dynamic visual cues, as those of the RDT, appears to be sensitive to age given that old adults were significantly more reliant on such contextual visual information than middle-aged adults as well. Middle-aged adults' scores on the GEFT also fell between those of young and old adults, being significantly different from both other age groups. This reveals a progressive change in the cognitive component of visual field dependence through adulthood. Interestingly, when extended to the influence on postural control, the effect of a dual mental or spatial task had similar consequences in both young and middle-aged adults, being different to that observed in old adults (Bernard-Demanze, Dumitrescu, Jimeno, Borel, & Lacour, 2009). In their study, Bernard-Demanze and colleagues (2009) found that the concurrent mental or spatial task improved postural control in young and middle-aged adults while postural control was impaired during dual-tasking in old adults. While performance on a more cognitive visuo-spatial task may be reduced in middle-age, when the task is performed concurrently with a postural task, the performance on the latter does not decrease, even if the postural stability impairment rate follows a linear trend with age (Du Pasquier et al., 2003).

Finally, while our middle-aged adults did not show impairments at the level of old adults in their ability to exploit the egocentric FoR for spatial orientation or self motion perception, they were influenced by the visual FoR during stepping in place under the more ecologic approaching flow. These participants drifted backwards, albeit to a lesser extent than old adults, while this behaviour was not seen in young adults. We note therefore that although there is an association between different manifestations of visual field dependence and between greater reliance on the visual FoR and reduced reliance on the egocentric FoR, their evolution trends with age are not identical nor is the associated repercussion on postural control. Further research should be conducted to better characterise these changes in middle-age, particularly given the large inter-individual variability observed in this group. This may lead to the identification of more precise transition points with respect to age and associated sensorimotor functions and behaviour as have been found in childhood and adolescence (Assaiante & Amblard, 1992; Assaiante & Amblard, 1995; Assaiante & Amblard, 1996; Sparto et al., 2006; Viel et al., 2009).

V.3 Uncertainty of the egocentric FoR in old adults and changes to the internal representations of the vertical and self

Throughout this work we have evoked the potential associations of greater reliance on the visual FoR as well as the potential risks for old adults. Our findings support previous research revealing a decreased ability to appropriately select and switch between different reference frames, both in young (Brady et al., 2012; Isableu et al., 2010) and old visual field dependent individuals (Bugnariu & Fung, 2007; Eikema et al., 2012; Eikema et al., 2013; Slaboda et al., 2011; Slaboda & Keshner, 2012). Furthermore, our work extends

previous findings by presenting an association of increased reliance on the visual FoR and decreased reliance on the egocentric FoR for both spatial orientation (RFT and RDT vs. RBT) and self-motion perception (visual self-motion quotient vs. natural drift), and by showing this progressive shift towards greater visual field dependence from young to middle-aged to old adulthood. Here we shall discuss our findings on reference frame reliance in the context of old adults' egocentric perception of their environment and how this may affect their own self-perception.

Beyond the influence of the visual field on spatial orientation and self-motion perception, our findings suggest that with age come alterations to the perception of the self, the body schema, which may be associated with a greater reliance on the visual FoR. We have several findings indicating a poorer quality (visual fixation instability) or exploitation (RBT erect and tilted, drift while stepping in place) of somatosensory cues with age and with reliance on the visual FoR. Somatosensory input plays a prominent role in the perception of one's subjective vertical, but also in the perception and control of one's orientation (Anastasopoulos et al., 1999; Barbieri et al., 2008; Barra et al., 2010; Bringoux, Nougier, Marin, Barraud, & Raphel, 2003; Bronstein, 1999; Vaugoyeau, Viel, Amblard, Azulay, & Assaiante, 2008; Yardley, 1990). Although we did not explicitly examine somatosensory function, we infer the existence of an age-related degradation in our old adults given the larger errors on the RBT while standing erect, the reduced Aubert effect while tilted, and the drift observed while stepping in place. Future studies in the context of aging and reference frame reliance should indeed investigate proprioceptive and kinaesthetic acuity (e.g. joint position sense, sensitivity to mass distributions and inertia alterations) in order to better understand the effect of such age-related degradation on the exploitation of the egocentric FoR for spatial orientation and self-motion perception in different tasks.

Studies have put forward the major somatosensory contribution in the use of internal models or body references for orientation perception and postural control as well (Barbieri et al., 2008; Barra et al., 2010; Roll et al., 1989). With age, changes come about the body schema, including the internal representation of one's postural vertical (Barbieri et al., 2010; Manckoundia et al., 2007) and affordances for motor actions and their control (Boisgontier & Nougier, 2013; Lafargue, Noël, & Luyat, 2013; Personnier, Paizis, Ballay, & Papaxanthis, 2008; Personnier, Ballay, & Papaxanthis, 2010). Our findings support these observations given the reduced somatosensory contribution to orientation and self-motion perception in old adults. The drift observed in our older and more visual field dependent individuals in the SIP task clearly reveals a lack of egocentric self-motion perception. The fact that old adults were not aware of their drift while stepping in place reveals a lacking contribution of somatosensory signals in the updating of old adult's body position and motion. Moreover, under conditions of optic flow, the drift was largely in the same direction as the stimulus. The somatosensory signals associated with this drift should have indicated that the self-initiated movement was not congruent with the one visually perceived. It would have been interesting to examine our participants' self-reported tilt during the RBT in addition to their verticality estimation to obtain clearer evidence of an alteration in self-orientation perception.

The association of both the reduced RBT scores and greater drift observed with reliance on the visual FoR is also consistent with reports in patients showing greater reliance on the visual FoR to compensate somatosensory deficits (Azulay et al., 1999; Azulay et al., 2002; Blouin et al., 1993; Bringoux et al., 2016; Bronstein et al., 1990; Funk et al., 2011; Vaugoyeau et al., 2007; Vaugoyeau & Azulay, 2010). As mentioned above, there is therefore justification in our associating greater visual field dependence in old age with a compensation for age-related somatosensory deficits. Moreover, somatosensory information processing is more complex for old adults as it increases the demand of attentional resources in integrating signals arising from multiple different sources and has been shown to be negatively affected by a concurrent cognitive task (Boisgontier et al., 2012). Indeed, not only does somatosensory information stem from various sources but different information may be used for sensorimotor control and spatial referencing, e.g. controlling the mass distribution, inertia or geometrical joint configuration (Bernardin et al., 2005; Isableu et al., 2009; Pagano & Turvey, 1995). Given the dangerous implications of poor self-perception regarding orientation with respect to vertical (Manckoundia et al., 2007) and affordances for action (Lafargue et al., 2013), it is important to be able to identify such changes in old adults as they may predict riskier behaviour with the further deterioration of somatosensory sensation and sensory integration with age. Moreover various deficits in somatosensation such as proprioceptive acuity, muscle strength and control of postural sway have been identified as risk factors for falls in old adults (Lord & Ward, 1994; Lord, Menz, & Tiedemann, 2003; Tinetti et al., 1988).

V.4 Perspectives on the identification of reliance on the visual FoR and the influence of the sensorimotor task

We next consider how excessive reliance on the visual FoR, or the upweighting of visual cues, may be revealed across sensorimotor tasks. The relative weight attributed to signals of a particular sensory modality may be inferred by observing how individuals respond when the cues associated with one or more modalities are modified or provide conflicting information with regard to the others (Gueguen et al., 2012). Greater reliance on the visual FoR is thus inferred by observing either the preferential use of visual cues for spatial orientation, self-orientation or self-motion or by observing a destabilisation in postural control when visual cues are perturbed. It should be noted that depending on the type of visual stimulation (e.g. oscillating scene, linear flow, direction and complexity of motion) or perturbation to vision (e.g. occluding part of the visual field, limiting dynamic cues via stroboscopic illumination) in conjunction with the task, different responses may be observed. In healthy individuals, perturbation to multiple senses or placing individuals in more posturally threatening situations (e.g. limiting the base of support) is usually necessary to examine how the CNS will upweight reliable somatosensory or vestibular input when visual information is conflicting. Indeed even though reweighting capacities degrade with age (Stelmach et al., 1989; Teasdale & Simoneau, 2001; Berard et al., 2012; Eikema et al., 2012), certain studies have found no age differences between young and

old adults' postural responses when the visual modality alone was perturbed, i.e. when the egocentric modalities were fully available and the dynamics of balance not compromised by difficult postural tasks (Bugnariu & Fung, 2007; Teasdale et al., 1991). By increasing the postural demands for stability, however, reliance on visual cues to maintain equilibrium become apparent, and this in earlier ages depending on the difficulty of the task (Choy et al., 2003).

Old adults' greater reliance on visual cues and reduced visuo-motor processing and control abilities (Chapman & Hollands, 2010; Mazaheri et al., 2015; Sotirakis, Kyvelidou, Mademli, Stergiou, & Hatzitaki, 2016) can pose threats to the adaptation requirements of changing environments and has been linked to falls (Barr et al., 2016; Chapman & Hollands, 2006; Chapman & Hollands, 2007; Lord & Webster, 1990; Young & Hollands, 2012). With this in mind it is important not only to identify visually-induced postural reaction and control differences between younger and older adults but also to place them in the context of the task and possible threat to daily life activities. Here we shall therefore consider the implications of visual field dependence described in the above sections and its manifestation across our sensorimotor tasks in the context of training perspectives as well as the methodological limitations of our study in assessing an increased visual contribution to postural control with age.

V.4.1 Perspectives for assessment, prevention and rehabilitation

The behaviour and factors associated with visual field dependence described so far suggest that increased individual differences with respect to reliance on the visual FoR should be taken into account in order to identify old adults that are more at risk and to personalise training protocols for rehabilitation. In young adults, greater reliance on the visual FoR was associated with a reduced ability to identify more reliable sensory signals and therefore appropriately reweight these for sensory integration (Gueguen et al., 2012). If the efficiency of young adults' interactions with their environment can be compromised by visual field dependence, it is especially important to identify and account for old adults' modes of spatial referencing, given the additional cognitive and sensorimotor deficits that appear with age. As mentioned above, downweighting or a deficit in the integration of somatosensory signals due may be detrimental for postural control in challenging situations. In addition, the correlation between greater visual field dependence and longer parallel visual attentional processing means that individuals more reliant on the visual FoR could be more sensitive to distracters in their visual field. Identifying greater reliance on the visual FoR at an earlier age may serve for prevention training in order to maintain autonomy. Moreover, the exacerbated reliance on the visual FoR of old adults as a compensation for age-related deficits may imply a poor exploitation of visual cues when these do not provide reliable information for postural control. Therefore accounting for greater visual field dependence as a compensation strategy rather than a preferred and efficient mode of

spatial referencing would also allow to better target the necessary functions to train in more risk-prone old adults, namely adaptation to sensory discordance, resistance to distraction and acuity of somatosensation. While assessments of fall risk and postural control take into account the different sensory deficits and contributions to balance maintenance in old age (Callisaya et al., 2009; Lord & Ward, 1994; Wrisley & Kumar, 2010), if vision is manipulated, this tends to be simply eye closure. There is a multitude of research employing dynamic or rotated visual scenes which reveal whether visual input is upweighted (Borger et al., 1999; Eikema et al., 2012; Franz et al., 2015; Isableu et al., 1998; Isableu et al., 1997; Poulain & Giraudet, 2008; Slaboda et al., 2011; Streepey et al., 2007; Yeh et al., 2014) and also showing promise for implementation in rehabilitation protocols due to the improvements in postural control observed after multiple exposures to sensory discordance including perturbed visual input in both young healthy individuals (Pavlou et al., 2011) and in old adults and patients (Bugnariu & Fung, 2007; Jeka et al., 2006; O'Connor et al., 2008; Slaboda, Lauer, & Keshner, 2013).

We already noted the importance of the sensorimotor task in revealing differences in reliance on the visual FoR. Our walking tasks were not threatening enough to postural stability, they did not require visual attention in order to safely walk across the walkway nor were there obstacles to avoid, therefore the task did not reflect the riskier aspects of old adults' interactions with their environment. Avoiding obstacles, negotiating stairs, circumventing moving individuals in crowds, these are all common and more threatening activities for old adults. The task of stepping in place, however, proved to be optimal in revealing differential sensitivities to optic flow and further revealed that reduced exploitation of the egocentric FoR extends to self-motion perception in participants more reliant on the visual FoR. This is particularly interesting given the practical implementation of a stepping in place task in order to examine sensitivity to different visual input as has been done with neck muscle proprioceptive input (Bove, Courtine, & Schieppati, 2002) or further assess adaptations over time, i.e. whether egocentric information on self-motion is eventually upweighted and the visual influence attenuated as found in other studies (Doumas & Krampe, 2010; Jeka et al., 2006). Moreover, the practical aspect of stepping in place is already being exploited in virtual environment protocols due to the closeness of the task to actual walking (Nilsson, Serafin, & Nordahl, 2014; Templeman, Denbrook, & Sibert, 1999).

V.4.2 Methodological limits and perspectives for future studies

While our protocols were developed to examine specific research questions, we note that methodological alternatives could lead to a closer examination of the influence of visual field dependence on daily interactions with one's environment or indeed clearer markers of reliance on the visual FoR while walking. Even if walking is more cognitively demanding in old age, it is still a fairly automatic skill and one that healthy individuals practice routinely throughout their lifetime. The initiation of gait poses greater threat to

postural stability (Polcyn et al., 1998; Assaiante et al., 2000), but apparently this was not enough to reveal a differential reliance on the visual FoR between our subjects. It is therefore possible that either a greater visual perturbation, concurrent perturbation of the somatosensory system via more posturally demanding tasks (Isableu et al., 2010) or modifying the size (Streepey et al., 2007), inclination (Slaboda & Keshner, 2012; Wang, Kenyon, & Keshner, 2010), dynamic stability (Keshner, Kenyon, & Langston, 2004; Mergner, Schweigart, Maurer, & Blümle, 2005) or firmness (Teasdale et al., 1991a; Nougier et al, 1997) of the support surface may be required to reveal such differences. Indeed, comparing the postural and walking tasks we observe a differential response to the visual stimuli provided as during quiet standing and stepping in place a greater influence of ground optic flow was revealed for self-motion perception in old and (during SIP) middle-aged adults. This is in agreement with the reported reduced influence of visual stimuli at higher locomotor speeds (Jahn, Strupp, Schneider, Dieterich, & Brandt, 2001) given the differences in body inertia from stance and stepping in place to walking and the respective hierarchical organisation in the control of these motor tasks (Jahn et al., 2004). Moreover, the visual-egocentric incongruence was greater during the postural tasks given that optic flow is a visual affordance providing speed and heading information when one moves through the environment and thus not associated with a (nearly) translation-less behaviour, therefore it makes sense that differential behaviour with regard to reliance on the visual FoR was observed on the postural tasks rather.

An important alternative in our protocol would be in the choice of visual stimuli that could prove more pertinent in assessing sensory reweighting in postural and locomotor tasks. A perturbation in the mediolateral rather than anteroposterior direction could have been used, given that increased reliance on the visual FoR in old adults' revealed in mediolateral instability (Franz et al., 2015; Yeh et al., 2014) and that old adults have a reduced ability to plan and execute mediolateral stepping adjustments (Chapman & Hollands, 2010). Examining the influence of visual stimuli in different locations of the visual field could also provide insight on the relative sensitivity to central versus peripheral and, indeed, lower peripheral visual cues. In addition, the use of complex visual stimuli may be more appropriate to create an experimental environment similar to that of daily life (Stergiou & Decker, 2011) and given that adaptability has been associated with organised complexity in sensorimotor function (Harrison & Stergiou, 2015) and changes in adaptation are particularly relevant in relying excessively on the visual FoR. Moreover, a finer processing of our data, including spectral analysis and dynamic stability of our variables could reveal sensitivities and changes in how visual cues are used that simple time-domain analyses cannot uncover. Indeed such analyses have been utilised to reveal differences regarding fall risk in old adults (Kang & Dingwell, 2008; Toebes, Hoozemans, Furrer, Dekker, & van Dieen, 2012) as they are more sensitive than traditional measures such as gait variability. Finally, future studies should consider including more visual field dependent young adults and more visual field *in*dependent old adults to better characterise the potential age-related changes that are associated with greater reliance on the visual FoR and also include assessments of the somatosensory and vestibular systems. The ideal, however, would be a longitudinal study of a cohort of young adults with individual differences in reference frame reliance in order to examine how reliance on the visual FoR may come to increase in old age

while also obtaining measures of different cognitive and sensorimotor functions in order to examine how these co-evolve.

V.5 General Conclusion

This thesis examined reliance on the visual frame of reference in young, middle-aged and old adults during different sensorimotor tasks. By considering on the one hand cognitive and sensorimotor degradations that occur with age, and on the other hand, the negative implications of reliance on the visual FoR, for example with respect to multisensory integration and adaptation abilities, we deemed it important to better characterise the associations of this mode of spatial referencing with sensorimotor control in old age.

We have shown that reliance on the visual FoR increases progressively throughout adulthood and is manifested in terms of both spatial orientation and self-motion perception while standing and stepping in place. Our work revealed an important association between the increased reliance on the visual FoR and reduced reliance on the egocentric FoR. This association was found for spatial orientation, as indicated by the negative correlation between subjective vertical estimation errors between the RFT and RDT tasks and the RBT (i.e. reduced Aubert effect) and for self-motion perception while stepping in place, as indicated by the positive correlation between optic flow sensitivity and natural drift (i.e. without visual stimulation). The reduced Aubert effect and greater natural drift observed with age indicate on their own that somatosensory information is either not salient enough or difficult to integrate in order to acquire orientation and self-motion information in old adults. These findings along with the correlation of greater visual fixation instability with increased visual field dependence and reduced egocentric dependence support our hypothesis that there is noise associated with somatosensory signals and their integration with age. The correlation found between greater visual field dependence and longer parallel attentional visual processing times, on the other hand, agree with our assumption that not only do old adults have difficulty in exploiting the egocentric FoR, but that relying excessively on the visual FoR also makes it more difficult to shift their mode of spatial referencing when necessary.

Our work also highlights the importance of i) designing appropriate protocols in order to identify excessive reliance on the visual FoR but also ii) taking visual field dependence into consideration for prevention or rehabilitation training protocols aimed at old adults' autonomy maintenance. While the visual self-motion quotient clearly identified old adults' reliance on the visual FoR while stepping in place, the walking tasks appeared to not be threatening enough to postural stability in order to obtain an obvious locomotor index of visual field dependence in old age. We did however reveal that the ability to systematically stabilise one's head in space, i.e. the optimal strategy for sensory integration, is lost with age. Interestingly, under conditions of imposed optic flow, an improvement in head stabilisation was observed, revealing that old

adults may still resort to this acquired coordination skill under situations of sensory discordance. Finally, we have discussed the importance of examining visual field dependence in old adults in order to provide more personalised care under practices aimed at improving their postural stability and motor control more generally. By assessing reliance on the visual FoR, appropriate protocols may be put in place with a focus on adaptability training and improving functions such as susceptibility to distraction and proprioceptive acuity. Moreover, we suggest that while reliance on the visual FoR in old age is associated with certain age-related deficits; increased reliance among old adults indicates, rather, a default mode of spatial referencing in order to compensate for more severe age-induced degradations. This latter case of visual field dependence should especially be identified and taken into account in training interventions given that it implies, on the one hand, a lack of adaptability and on the other, an exploitation of the visual FoR that may not always be optimal.

Fin.

VI. *Appendix 1: Résumé Détaillé*

Le processus de vieillissement entraîne une dégradation à la fois des systèmes sensoriels et des processus centraux de traitement des signaux sensoriels qui peuvent se manifester dans les tâches de la vie quotidienne par une perte d'autonomie, et des risques accrus de chute notamment chez les plus âgés. Parmi les facteurs identifiés comme facteurs de risque de chute, Ambrose et al. (2013) citent la démarche rigide et protectrice, la force musculaire réduite, des atteintes de la fonction visuelle se traduisant par une altération de la perception des profondeurs, une diminution de la vision stéréoscopique ainsi que des capacités d'attention (d'attention divisée en particulier) et des fonctions exécutives. Ce projet de recherche a été conçu en considérant ces risques et en prenant en compte la croissance rapide de la population âgée (World Health Organisation, 2015). Bien que les études sur la posture et la marche des seniors soient abondantes, il reste des questions concernant l'augmentation de la dépendance au cadre de référence visuel avec l'âge et, précisement, l'influence de celle-ci sur le contrôle sensorimoteur. Par exemple, les individus avec une plus grande dépendance au référentiel visuel (DRV) adoptent un mode de rigidification intersegmentaire afin de se stabiliser, et s'orienter (Isableu, Ohlmann, Crémieux, & Amblard, 2003), montrent des difficultés à stabiliser leur tête sur l'espace en postures difficiles, et sont plus lents à s'adapter à des situations de discordance sensorielles (Brady et al., 2012; Isableu et al., 2010). Si nous considérons ces comportements en plus des effets liés à l'âge, l'augmentation de la DRV chez les seniors peut mener à des difficultés dans les activités de la vie quotidienne, la DRV étant considérée comme un facteur de risque de chute (Lord & Webster, 1990). Les travaux présentés dans ce manuscrit visent i) à examiner si des effets d'âge sur la cognition et/ou la sensorimotricité sont également liés à une augmentation de la DRV, ii) à étudier l'évolution du rôle de la surface d'appui dans le contrôle et la régulation des activités posturales et locomotrices au cours de l'avancée en âge, et en particulier iii) à expliquer si les différences interindividuelles observées dépendent des modes préférentiels de référentiation spatiale (visuel vs. somatosensoriel). Le rôle déterminant du sol comme référentiel spatial pour s'orienter, se stabiliser, et se déplacer, sera plus particulièrement étudié en manipulant expérimentalement les informations liées à sa composante visuelle (i.e., structuration du sol, vitesse et direction des flux optiques linéaires projetés au sol), et/ou somatosensorielle (notamment cutanée plantaire : permanence vs intermittence des contacts podaux). La discordance des caractéristiques des flux optiques projetés au sol, par rapport aux invariances multimodales attendues dans les conditions de référence écologique, devrait permettre de mieux comprendre l'évolution avec l'âge, et en particulier chez les seniors, des modes préférentiels de référentiation spatiale dans le contrôle sensorimoteur de la perception à la marche. L'objectif vise à répondre à la question principale suivante : Est-ce que l'augmentation signalée de la dépendance au référentiel visuel constitue une adaptation avec l'âge vers un mode de référentiation spatiale préféré ou est-ce une compensation vis-à-vis des déficits liés à l'âge ?

Une étude transversale a été réalisée comprenant l'inclusion de jeunes adultes (23 - 44 ans), d'adultes d'âge moyen (45 - 64 ans), et de seniors (70 - 82 ans). Nous avons tout d'abord examiné des facteurs cognitifs et sensorimoteurs éventuellement associés à une plus grande DRV avec l'âge (Chapitre 2). Nous avons confirmé les résultats de la littérature montrant une augmentation de la DRV chez les seniors, notamment à partir de l'âge moyen à l'aide du test du cadre et de la baguette (*Rod-and-Frame Test*, RFT), du disque et de la baguette (*Rod-and-Disc Test* (RDT) et des figures encastrées (*Group Embedded Figures Test*, GEFT). De plus, nous avons mis en évidence une association entre une plus grande DRV et i) une réduction de la dépendance au référentiel égocentré (DRE), indiquée par une réduction de l'effet Aubert dans l'estimation de la verticale subjective (*Rod-and-Body Test*, RBT), ii) une diminution des capacités de traitement d'attention visuelle parallèle, indiquée par des temps plus lents pour accomplir le test du champ visuel attentionnel – Useful Field Of View® et iii) une plus grande instabilité de fixation visuelle, indiquée par une plus grande dispersion des positions de regard pendant une tâche de fixation.

Par la suite, nous avons étudié les comportements d'orientation et de stabilisation de nos participants pendant des tâches posturales (Chapitre 3) et locomotrices (Chapitre 4) induits par différentes conditions de flux optique linéaire projetées au sol. Dans le Chapitre 3 nos participants se tenaient en posture érigée ou marchaient sur place en étant exposé à 1- un flux naturel (sans stimulation visuelle) ; 2- une stimulation visuelle statique (un patron de pavés immobile), et un flux optique soit 3- en approche ou 4- en recul, le patron se rapprochant ou s'éloignant du participant, respectivement. La vitesse des flux optiques était déterminée en fonction de la vitesse moyenne de marche de chaque participant tel que: vitesse_flux = + /- 0.5 * vitesse_participant (-ve pour flux en approche et +ve pour flux en recul) pour prendre compte des différences liées à l'âge sur la vitesse de marche et ainsi fournir un stimulus dont le gain visuel (0.5) était identique pour tous nos participants. Les résultats principaux montrent que les flux optiques ont provoqué des dérives antéropostérieures de la tête, du tronc et du centre de pression (CdP), principalement lors de la condition de marche sur place. Les dérives pendant la marche sur place étaient plus marquées chez les seniors par rapport aux participants plus jeunes, et ce à la fois dans les conditions de flux ainsi que sans stimulation visuelle (dérive naturelle). De plus, en condition de flux en approche nous avons observé des dérives du CdP chez les adultes d'âge moyen et les seniors, mais pas chez les jeunes adultes. Le plus important effet *directionnel* induit par le flux optique a été observé au niveau de la vitesse de dérive du CdP par rapport à la vitesse du flux, nommé quotient de mouvement-propre visuel. Ce quotient était par ailleurs associé à i) une DRV supérieure, ii) une plus grande dérive naturelle, i.e. indicateur de réduction de la perception du mouvement- propre égocentrée, et iii) une DRE réduite. Pris ensemble nos résultats montrent que la dépendance au référentiel visuel s'étend de l'orientation spatiale à la perception du mouvement-propre et suggèrent que l'avancée en âge s'accompagne d'une réduction de la perception égocentrée du mouvement propre par rapport au sol, les seniors se fiant plutôt aux informations visuelles de mouvement fournies.

Dans le chapitre 4, nous avons étudié l'influence de ces mêmes flux sur le contrôle des paramètres de la marche et sur la stabilisation de la tête au cours de la marche. Les essais de marche étaient enregistrés à la

suite des tâches posturales mentionnées ci-dessus. La dépendance au cadre de référence visuel s'est manifestée chez les seniors dans les conditions de 1) flux naturel par une stratégie d'abaissement de la tête et une capacité réduite de stabilisation de la tête sur l'espace dont on peut penser que ces comportements visaient à maximiser l'utilisation des indices visuels disponibles, et 2) flux optiques visuels imposés, par une réorientation du tronc vers l'arriere sous flux en approche et une augmentation de la fréquence du pas sous les deux directions de flux. Les résultats montrent aussi une amélioration de la stabilisation de la tête vers une stratégie de stabilisation de la tête sur l'espace en conditions imposées de stimulation visuelle suggérant que le renforcement artificiel du flux optique mène à une adaptation posturale pour optimiser l'intégration des informations sensorielles pendant la marche.

Nos résultats complètent les connaissances actuelles sur l'évolution des déterminants du contrôle sensorimoteur avec l'avancée en 'âge et en particulier sur la manière dont la DRV se manifeste en fonction de la tâche perceptivo-motrice. Il semble évident que cette dépendance est associée à une réduction de l'exploitation du cadre de référence égocentrée pour l'orientation spatiale et la perception du mouvement-propre qui peut relever de déficits (d'une altération ou atténuation de l'acuité) du système somatosensoriel avec l'âge. L'altération du schéma corporel est ainsi discutée également. Enfin, nos résultats s'appuient sur ceux d'études précédentes montrant que la DRV chez les seniors est associée à un manque de flexibilité de l'adaptation et de la repondération sensorielle dynamique (Berard, Fung, & Lamontagne, 2012; Eikema, Hatzitaki, Konstantakos, & Papaxanthis, 2013). Nous considérons donc que la DRV exacerbée avec les effets d'âge est indicative d'une compensation plutôt qu'un mode de référentiation préféré. Notre travail fourni des pistes de réflexion pour identifier la DRV exacerbée et pour la conception de protocoles d'entraînement pour des seniors plus atteints, tenant compte des différences individuelles dans l'orientation spatiale.

VII. *Appendix 2: Data in complement to Chapter 4*

VII.1 Baseline locomotor data

The tables below provide data measured during the control condition for the locomotor parameters well as the head and trunk mean pitch orientation and oscillation amplitudes in all three rotation planes as.

Table VI.1: Mean values with standard deviations for locomotor parameters measured during the control condition. Values indicated for both QS-first and SIP-first trials for each age group.

Index	Gait Cycle	QS-first trials			SIP-first trials		
		YA	MA	OA	YA	MA	OA
Step length (cm)	Initial cycle	72.96 ± 7.68	68.27 ± 6.69	**55.30 ± 7.88 *†**	38.09 ± 8.07	38.81 ± 11.16	**29.82 ± 5.41 *†**
	Steady state gait	76.77 ± 8.67	72.34 ± 4.98	**63.34 ± 5.99 *†**	74.19 ± 8.71	70.64 ± 7.06	**59.65 ± 6.21 *†**
Step width (cm)	Initial cycle	10.17 ± 2 .10	8.62 ± 2.65	10.41 ± 2.91	9.90 ± 2.05	8.32 ± 2.54	9.23 ± 2.14
	Steady state gait	7.00 ± 3.21	5.01 ± 3.57	4.41 ± 3.44	4.18 ± 2.26	3.73 ± 2.43	4.49 ± 3.33
Cadence (steps/min)	Initial cycle	103.00 ± 7.84	102.21 ± 8.35	96.80 ± 9.03	116.12 ± 11.31	120.81 ± 15.38	110.64 ± 15.83
	Steady state gait	113.42 ± 11.19	112.53 ± 9.86	107.25 ± 11.03	109.71 ± 9.23	113.99 ± 9.63	**105.37 ± 12.07 †**
Walking Speed (m/s)	Initial cycle	0.81 ± 0.14	0.74 ± 0.13	**0.55 ± 0.08 *†**	0.47 ± 0.11	0.49 ± 0.15	**0.33 ± 0.09*†**
	Steady state gait	1.25 ± 0.21	1.15 ± 0.15	**0.94 ± 0.13 *†**	1.17 ± 0.18	1.11 ± 0.17	**0.85 ± 0.13 *†**

*: significant difference with YA
†: significant difference with MA

Table VI.2: Mean values with standard deviations for head and trunk pitch orientation and amplitudes of oscillations in all three rotation planes measured during the control condition. Values indicated for both QS-first and SIP-first trials for each age group.

Index		Gait Cycle	QS-first trials			SIP-first trials		
			YA	*MA*	*OA*	*YA*	*MA*	*OA*
Mean Pitch Orientation (°)	Head	Initial cycle	85.20± 3.92	87.65± 3.10	81.07± 7.73 †	88.07 ± 4.74	90.91 ± 3.93	83.80 ± 5.75 *†
		Steady state gait	85.94 ± 2.78	87.59 ± 3.39	84.21 ± 4.29 †	87.92 ± 4.91	90.41 ± 4.03	84.27 ± 5.47 †
	Trunk	Initial cycle	82.59 ±1.62	83.94 ± 2.61	84.06± 2.25	83.78 ± 2.22	84.05 ± 2.52	84.33 ± 2.60
		Steady state gait	84.07 ± 1.77	85.45 ± 2.50	85.12 ± 2.15	82.97 ± 2.49	83.93 ± 3.09	83.94 ± 2.42
Amplitude of Oscillations in Pitch (°)	Head	Initial cycle	2.21 ± 1.37	2.06 ± 1.07	3.01 ± 3.37	2.06 ± 1.18	1.97 ± 0.90	3.62 ± 3.82
		Steady state gait	2.02 ± 1.02	2.12 ± 1.37	2.47 ± 1.88	2.30 ± 0.93	2.23 ± 1.69	2.95 ± 1.92
	Trunk	Initial cycle	1.79 ± 0.59	1.54 ± 0.68	1.41 ± 0.71	1.56 ± 0.45	1.46 ± 0.49	1.25 ± 0.59
		Steady state gait	1.46 ± 0.39	1.36 ± 0.34	1.20 ± 0.37	1.97 ± 0.70	1.78 ± 0.53	1.37 ± 0.44 *
Amplitude of Oscillations in Roll (°)	Head	Initial cycle	1.33 ± 0.70	1.23 ± 0.47	0.89 ± 0.34 *	1.34 ± 0.6	1.15 ± 0.53	0.87 ± 0.31 *
		Steady state gait	1.41 ± 0.52	1.50 ± 0.68	1.13 ± 0.59	1.72 ± 0.58	1.56 ± 0.69	1.18 ± 0.49 *
	Trunk	Initial cycle	1.50 ± 0.52	1.39 ± 0.55	0.98 ± 0.41 *†	1.34 ± 0.63	1.30 ± 0.77	0.90 ± 0.35
		Steady state gait	1.36 ± 0.44	1.23 ± 0.34	0.96 ± 0.28 *	1.42 ± 0.51	1.41 ± 0.42	1.03 ± 0.33 *†
Amplitude of Oscillations in Yaw (°)	Head	Initial cycle	2.18 ± 0.73	1.93 ± 0.71	1.56 ± 0.75 *	2.03 ± 0.67	1.60 ± 0.54	1.49 ± 0.58 *
		Steady state gait	1.81 ± 0.49	1.85 ± 0.64	1.70 ± 0.96	2.18 ± 0.50	1.99 ± 0.77	2.04 ± 1.09
	Trunk	Initial cycle	2.79 ± 0.62	2.10 ± 0.76 *	1.61 ± 0.71 *	2.30 ± 0.85	2.05 ± 0.69	1.52 ± 0.48 *
		Steady state gait	2.49 ± 0.70	2.36 ± 0.61	1.99 ± 0.62 *	2.66 ± 0.71	2.46 ± 0.78	2.18 ± 0.69

*: significant difference with YA
†: significant difference with MA

VII.2 Anchoring Index t-test results

Table VI.3: T-test results comparing AI values in Pitch to zero. The postural (quiet standing vs. stepping in place) and walking task are indicated, including the initial postural condition for the walking trial (i.e. QS-first or SIP-first) for each visual stimulation condition and age group.

Postural/Walking Task			YA		MA		OA	
			AI value	p	AI value	p	AI value	p
Natural Flow	Quiet Standing		<0	0.000	<0	0.000	<0	0.000
	Stepping in Place		>0	0.000	>0	0.000	~0	N/S
	IGC	QS-first	~0	N/S	>0	0.000	~0	N/S
		SIP-first	~0	N/S	~0	N/S	<0	0.001
	SSG	QS-first	~0	N/S	~0	N/S	~0	N/S
		SIP-first	~0	N/S	>0	0.005	~0	N/S
Static Stimulation	Quiet Standing		<0	0.000	<0	0.000	<0	0.000
	Stepping in Place		>0	0.004	>0	0.000	~0	N/S
	IGC	QS-first	~0	N/S	~0	N/S	~0	N/S
		SIP-first	~0	N/S	~0	N/S	~0	N/S
	SSG	QS-first	>0	0.002	~0	N/S	~0	N/S
		SIP-first	~0	N/S	>0	0.004	~0	N/S
Approaching Flow	Quiet Standing		<0	0.000	<0	0.006	<0	0.004
	Stepping in Place		>0	0.000	>0	0.000	~0	N/S
	IGC	QS-first	>0	0.003	>0	0.002	~0	N/S
		SIP-first	~0	N/S	>0	0.000	~0	N/S
	SSG	QS-first	>0	0.002	~0	N/S	~0	N/S
		SIP-first	~0	N/S	~0	N/S	>0	0.003
Receding Flow	Quiet Standing		<0	0.000	<0	0.000	<0	0.000
	Stepping in Place		>0	0.000	>0	0.001	~0	N/S
	IGC	QS-first	>0	0.005	~0	N/S	~0	N/S
		SIP-first	>0	0.001	~0	N/S	~0	N/S
	SSG	QS-first	~0	N/S	~0	N/S	~0	N/S
		SIP-first	>0	0.002	>0	0.001	>0	0.012

Head Stabilisation in Space Strategy

Head Stabilisation on the Trunk Strategy (*en bloc*)

No Systematic Head Stabilisation Strategy

Table VI.4: T-test results comparing AI values in Roll to zero. The postural (quiet standing vs. stepping in place) and walking task are indicated, including the initial postural condition for the walking trial (i.e. QS-first or SIP-first) for each visual stimulation condition and age group.

			YA		MA		OA	
Postural/Walking Task			AI value	p	AI value	p	AI value	p
Natural Flow	Quiet Standing		<0	0.000	<0	0.000	<0	0.000
	Stepping in Place		~0	N/S	~0	N/S	~0	N/S
	IGC	QS-first	~0	N/S	>0	0.000	>0	0.003
		SIP-first	~0	N/S	>0	0.001	~0	N/S
	SSG	QS-first	>0	0.005	>0	0.001	~0	N/S
		SIP-first	>0	0.002	>0	0.002	~0	N/S
Static Stimulation	Quiet Standing		<0	0.000	<0	0.001	<0	0.000
	Stepping in Place		~0	N/S	~0	N/S	~0	N/S
	IGC	QS-first	>0	0.000	>0	0.000	>0	0.000
		SIP-first	>0	0.002	>0	0.006	>0	0.001
	SSG	QS-first	>0	0.000	>0	0.000	>0	0.009
		SIP-first	>0	0.001	>0	0.001	>0	0.013
Approaching Flow	Quiet Standing		<0	0.000	<0	0.000	<0	0.000
	Stepping in Place		~0	N/S	~0	N/S	~0	N/S
	IGC	QS-first	>0	0.004	>0	0.004	>0	0.007
		SIP-first	~0	N/S	>0	0.004	~0	N/S
	SSG	QS-first	>0	0.000	>0	0.000	~0	N/S
		SIP-first	>0	0.004	>0	0.001	~0	N/S
Receding Flow	Quiet Standing		<0	0.000	<0	0.001	<0	0.000
	Stepping in Place		~0	N/S	~0	N/S	~0	N/S
	IGC	QS-first	>0	0.009	>0	0.001	>0	0.003
		SIP-first	~0	N/S	>0	0.001	~0	N/S
	SSG	QS-first	>0	0.001	>0	0.001	>0	0.011
		SIP-first	>0	0.000	>0	0.001	~0	N/S

Head Stabilisation in Space Strategy

Head Stabilisation on the Trunk Strategy (*en bloc*)

No Systematic Head Stabilisation Strategy

VIII. *Thesis Valorisation*

Journal Papers

Agathos, C. P., Bernardin, D., Huchet, D., Scherlen, A. C., Assaiante, C., & Isableu, B. (2015). Sensorimotor and cognitive factors associated with the age-related increase of visual field dependence: a cross-sectional study. *AGE, 37,* 1-19 doi: http://dx.doi.org/10.1007/s11357-015-9805-x

Agathos, C. P., Bernardin, D., Baranton, K., Assaiante, C., & Isableu, B. Drifting while stepping in place in old adults: association of self-motion perception with reference frame reliance and ground optic flow sensitivity. - Under revision to be submitted in Neuroscience:

Conference Presentations

Agathos, C. P., Bernardin, D., Baranton, K., Assaiante, C., & Isableu, B. Centre of pressure drift when stepping in place increases with age, sensitivity to optic flow and perceptual reference frame reliance. *International Workshop on Aging in the Neuro-Musculo-Skeletal System*, 15-17 March 2016, Marseille, France – Oral presentation

Agathos, C. P., Bernardin, D., Huchet, D., Scherlen, A. C., Assaiante, C., & Isableu, B. Cognitive and sensorimotor factors associated with visual field dependence in the context of aging. *16th ACAPS conference*, 26-28 October 2015, Nantes, France – Oral presentation

Agathos, C. P., Bernardin, D., Huchet, D., Scherlen, A. C., Assaiante, C., & Isableu, B. Factors associated with the increased perceptual reliance on the visual reference frame with age. *International Society for Posture and Gait Research World Congress* (ISPGR 2015), 28 June – 2 July 2015, Seville, Spain – Poster presentation

References

Abrahamova, D. & Hlavacka, F. (2008). Age-related changes of human balance during quiet stance. *Physiological Research, 57,* 957.

Agathos, C. P., Bernardin, D., Huchet, D., Scherlen, A. C., Assaiante, C., & Isableu, B. (2015). Sensorimotor and cognitive factors associated with the age-related increase of visual field dependence: a cross-sectional study. *AGE, 37,* 1-19.

Aksan, N., Anderson, S. W., Dawson, J. D., Johnson, A. M., Uc, E. Y., & Rizzo, M. (2012). Cognitive Functioning Predicts Driver Safety On Road-Tests 1 and 2 Years Later. *Journal of the American Geriatrics Society, 60,* 99-105.

Amblard, B., Assaiante, C., Fabre, J. C., Mouchnino, L., & Massion, J. (1997). Voluntary head stabilization in space during oscillatory trunk movements in the frontal plane performed in weightlessness. *Experimental brain research, 114,* 214-225.

Amblard, B., Crémieux, J., Marchand, A. R., & Carblanc, A. (1985). Lateral orientation and stabilization of human stance: static versus dynamic visual cues. *Exp Brain Res, 61,* 21-37.

Ambrose, A. F., Paul, G., & Hausdorff, J. M. (2013). Risk factors for falls among older adults: a review of the literature. *Maturitas, 75,* 51-61.

Anastasopoulos, D., Bronstein, A., Haslwanter, T., Fetter, M., & Dichgans, J. (1999). The role of somatosensory input for the perception of verticality. *Ann.N.Y.Acad.Sci., 871,* 379-383.

Anstis, S. (1995). Aftereffects from jogging. *Experimental brain research, 103,* 476-478.

Assaiante, C. & Amblard, B. (1992). Peripheral vision and age-related differences in dynamic balance. *Human Movement Science, 11,* 533-548.

Assaiante, C. & Amblard, B. (1993). Ontogenesis of head stabilization in space during locomotion in children: influence of visual cues. *Exp Brain Res, 93,* 499-515.

Assaiante, C. & Amblard, B. (1995). An ontogenetic model for the sensorimotor organization of balance control in humans. *Human Movement Science, 14,* 13-43.

Assaiante, C. & Amblard, B. (1996). Visual factors in the child's gait: effects on locomotor skills. *Perceptual and motor skills, 83,* 1019.

Assaiante, C., Mallau, S., Viel, S., Jover, M., & Schmitz, C. (2005). Development of Postural Control in Healthy Children: A Functional Approach. *Neural Plasticity, 12,* 109-118.

Assaiante, C., Woollacott, M., & Amblard, B. (2000). Development of postural adjustment during gait initiation: kinematic and EMG analysis. *Journal of Motor Behavior, 32,* 211-226.

Azulay, J. P. (1998). *Contrôle visuel de la locomotion chez le parkinsonien.* Doctoral Thesis, Université d'Aix-Marseille II.

Azulay, J. P., Mesure, S., Amblard, B., Blin, O., Sangla, I., & Pouget, J. (1999). Visual control of locomotion in Parkinson's disease. *Brain, 122,* 111-120.

Azulay, J. P., Mesure, S., Amblard, B., & Pouget, J. (2002). Increased visual dependence in Parkinson's disease. *Perceptual and motor skills, 95,* 1106-1114.

Azulay, J. P., Mesure, S., & Blin, O. (2006). Influence of visual cues on gait in Parkinson's disease: Contribution to attention or sensory dependence? *Journal of the Neurological Sciences, 248,* 192-195.

Bagust, J., Docherty, S., Haynes, W., Telford, R., & Isableu, B. (2013). Changes in Rod and Frame Test Scores Recorded in Schoolchildren during Development - A Longitudinal Study. *PloS one, 8,* e65321.

Bagust, J., Docherty, S., & Razzak, R. A. (2013). Rod and frame alignment times increase when the frame is tilted. *Psychology and Behavioral Sciences, 2,* 66-72.

Bailleux, C., Marendaz, C., & Ohlmann, T. (1990). Selection of reference frames in four orientation tasks in relation to postural-gravitational constraints and individual habits in spatial orientation. *Perception, 19,* 381.

Ball, K., Owsley, C., Sloane, M. E., Roenker, D. L., & Bruni, J. R. (1993). Visual attention problems as a predictor of vehicle crashes in older drivers. *Investigative Ophthalmology & Visual Science, 34,* 3110-3123.

Ball, K. K., Beard, B. L., Roenker, D. L., Miller, R. L., & Griggs, D. S. (1988). Age and visual search: Expanding the useful field of view. *JOSA A, 5,* 2210-2219.

Ball, K. K., Roenker, D. L., Wadley, V. G., Edwards, J. D., Roth, D. L., McGwin, G. et al. (2006). Can High-Risk Older Drivers Be Identified Through Performance-Based Measures in a Department of Motor Vehicles Setting? *Journal of the American Geriatrics Society, 54,* 77-84.

Ball, K., Owsley, C., & Beard, B. (1990). Clinical visual perimetry underestimates peripheral field problems in older adults. *Clinical Vision Sciences, 5,* 113-125.

Barbieri, G., Gissot, A. S., Fouque, F., Casillas, J. M., Pozzo, T., & Pérennou, D. (2008). Does proprioception contribute to the sense of verticality? *Exp Brain Res, 185,* 545-552.

Barbieri, G., Gissot, A. S., & Pérennou, D. (2010). Ageing of the postural vertical. *AGE, 32,* 51-60.

Barr, C. J., McLoughlin, J. V., van den Berg, M. E. L., Sturnieks, D. L., Crotty, M., & Lord, S. R. (2016). Visual field dependence is associated with reduced postural sway, dizziness and falls in older people attending a falls clinic. *The journal of nutrition, health & aging,* 1-5.

Barra, J., Marquer, A., Joassin, R., Reymond, C., Metge, L., Chauvineau, V. et al. (2010). Humans use internal models to construct and update a sense of verticality. *Brain, 133,* 3552-3563.

Barrett, G. V., Cabe, P. A., & Thornton, C. L. (1968). Visual functioning and embedded figures test performance. *Perceptual and motor skills, 26,* 40.

Barrett, G. V. & Thornton, C. L. (1968). Relationship between perceptual style and driver reaction to an emergency situation. *Journal of Applied Psychology, 52,* 169.

Baumberger, B., Flückiger, M., & Roland, M. (2000). Walking in an environment of moving ground texture. *Japanese Psychological Research, 42,* 238-250.

Baumberger, B., Isableu, B., & Flückiger, M. (2004). The visual control of stability in children and adults: postural readjustments in a ground optical flow. *Experimental brain research, 159,* 33-46.

Bednarek, H. & Orzechowski, J. (2008). Cognitive and temperamental predictors of field dependence-independence. *Polish Psychological Bulletin, 39,* 54-65.

Berard, J. R., Fung, J., & Lamontagne, A. (2011). Evidence for the use of rotational optic flow cues for locomotor steering in healthy older adults. *J.Neurophysiol., 106,* 1089-1096.

Berard, J. R., Fung, J., McFadyen, B. J., & Lamontagne, A. (2009). Aging affects the ability to use optic flow in the control of heading during locomotion. *Exp Brain Res, 194,* 183-190.

Berard, J., Fung, J., & Lamontagne, A. (2012). Impact of aging on visual reweighting during locomotion. *Clinical Neurophysiology, 123,* 1422-1428.

Bernard-Demanze, L., Dumitrescu, M., Jimeno, P., Borel, L., & Lacour, M. (2009). Age-related changes in posture control are differentially affected by postural and cognitive task complexity. *Current aging science, 2,* 135-149.

Bernardin, D., Isableu, B., Fourcade, P., & Bardy, B. t. G. (2005). Differential exploitation of the inertia tensor in multi-joint arm reaching. *Experimental brain research, 167,* 487-495.

Bernier, P. M., Chua, R., & Franks, I. M. (2005). Is proprioception calibrated during visually guided movements? *Experimental brain research, 167,* 292-296.

Berthoz, A. & Pozzo, T. (1988). Intermittent head stabilization during postural and locomotory tasks in humans. *Posture and gait: development, adaptation and modulation.Elsevier, Amsterdam,* 189-198.

Beurskens, R. & Bock, O. (2012). Age-related decline of peripheral visual processing: the role of eye movements. *Exp Brain Res, 217,* 117-124.

Bian, Z., Braunstein, M. L., & Andersen, G. J. (2005). The ground dominance effect in the perception of 3-D layout. *Perception & psychophysics, 67,* 802-815.

Blouin, J., Bard, C., Teasdale, N., Paillard, J., Fleury, M., Forget, R. et al. (1993). Reference systems for coding spatial information in normal subjects and a deafferented patient. *Experimental brain research, 93,* 324-331.

Boisgontier, M. P., Olivier, I., Chenu, O., & Nougier, V. (2012). Presbypropria: the effects of physiological ageing on proprioceptive control. *AGE, 34,* 1179-1194.

Boisgontier, M. & Nougier, V. (2013). Ageing of internal models: from a continuous to an intermittent proprioceptive control of movement. *AGE, 35,* 1339-1355.

Bonan, I. V., Colle, F. M., Guichard, J. P., Vicaut, E., Eisenfisz, M., Huy, P. T. B. et al. (2004). Reliance on visual information after stroke. Part I: Balance on dynamic posturography. *Archives of physical medicine and rehabilitation, 85,* 268-273.

Borel, L., Lopez, C., Péruch, P., & Lacour, M. (2008). Vestibular syndrome: A change in internal spatial representation. *Neurophysiologie Clinique/Clinical Neurophysiology, 38,* 375-389.

Borger, L. L., Whitney, S. L., Redfern, M. S., & Furman, J. M. (1999). The influence of dynamic visual environments on postural sway in the elderly. *J.Vestib.Res, 9,* 197-205.

Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S. et al. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain: a journal of neurology, 124,* 1182.

Bove, M., Courtine, G., & Schieppati, M. (2002). Neck muscle vibration and spatial orientation during stepping in place in humans. *Journal of neurophysiology, 88,* 2232-2241.

Brady, R. A., Peters, B. T., Batson, C. D., Ploutz-Snyder, R., Mulavara, A. P., & Bloomberg, J. J. (2012). Gait adaptability training is affected by visual dependency. *Experimental brain research, 220,* 1-9.

Brady, R. A., Peters, B. T., & Bloomberg, J. J. (2009). Strategies of healthy adults walking on a laterally oscillating treadmill. *Gait & Posture, 29,* 645-649.

Brandt, T., Krafczyk, S., & Malsbenden, I. (1981). Postural Imbalance with Head Extension: Improvement by Training as a Model for Ataxia Therapy. *Annals of the New York Academy of Sciences, 374,* 636-649.

Brandt, T., Bartenstein, P., Janek, A., & Dieterich, M. (1998). Reciprocal inhibitory visual-vestibular interaction. Visual motion stimulation deactivates the parieto-insular vestibular cortex. *Brain, 121,* 1749-1758.

Bringoux, L., Bourdin, C., Lepecq, J. C., Sandor, P. M., Pergandi, J. M., & Mestre, D. (2009). Interaction between reference frames during subjective vertical estimates in a tilted immersive virtual environment. *Perception, 38,* 1053.

Bringoux, L., Nougier, V., Marin, L., Barraud, P. A., & Raphel, C. (2003). Contribution of somesthetic information to the perception of body orientation in the pitch dimension. *The Quarterly Journal of Experimental Psychology Section A, 56,* 909-923.

Bringoux, L., Scotto Di Cesare, C. +., Borel, L., Macaluso, T., & Sarlegna, F. R. (2016). Do Visual and Vestibular Inputs Compensate for Somatosensory Loss in the Perception of Spatial Orientation? Insights from a Deafferented Patient. *Frontiers in human neuroscience, 10,* 181.

Bronstein, A. M. (1988). Evidence for a vestibular input contributing to dynamic head stabilization in man. *Acta Oto-Laryngologica, 105,* 1-6.

Bronstein, A. M., Hood, J. D., Gresty, M. A., & Panagi, C. (1990). Visual control of balance in cerebellar and parkinsonian syndromes. *Brain, 113,* 767-779.

Bronstein, A. M., Yardley, L., Moore, A. P., & Cleeves, L. (1996). Visually and posturally mediated tilt illusion in Parkinson's disease and in labyrinthine defective subjects. *Neurology, 47,* 651-656.

Bronstein, A. M. (1999). The interaction of otolith and proprioceptive information in the perception of verticality: the effects of labyrinthine and CNS disease. *Annals of the New York Academy of Sciences, 871,* 324-333.

Bugnariu, N. & Fung, J. (2007). Aging and selective sensorimotor strategies in the regulation of upright balance. *Journal of NeuroEngineering and Rehabilitation (JNER), 4,* 19.

Callisaya, M. L., Blizzard, L., Schmidt, M. D., McGinley, J. L., Lord, S. R., & Srikanth, V. K. (2009). A population-based study of sensorimotor factors affecting gait in older people. *Age and Ageing, 38,* 290-295.

Campbell, A. J., Reinken, J., Allan, B. C., & Martinez, G. S. (1981). Falls in old age: a study of frequency and related clinical factors. *Age and Ageing, 10,* 264-270.

Chao, L. L. & Knight, R. T. (1997). Prefrontal deficits in attention and inhibitory control with aging. *Cerebral cortex, 7,* 63-69.

Chapman, G. J. & Hollands, M. A. (2006). Evidence for a link between changes to gaze behaviour and risk of falling in older adults during adaptive locomotion. *Gait & Posture, 24,* 288-294.

Chapman, G. J. & Hollands, M. A. (2007). Evidence that older adult fallers prioritise the planning of future stepping actions over the accurate execution of ongoing steps during complex locomotor tasks. *Gait & Posture, 26,* 59-67.

Chapman, G. J. & Hollands, M. A. (2010). Age-related differences in visual sampling requirements during adaptive locomotion. *Experimental brain research, 201,* 467-478.

Chou, Y. h., Wagenaar, R. C., Saltzman, E., Giphart, J. E., Young, D., Davidsdottir, R. et al. (2009). Effects of optic flow speed and lateral flow asymmetry on locomotion in younger and older adults: a virtual reality study. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences,* gbp003.

Choy, N. L., Brauer, S., & Nitz, J. (2003). Changes in postural stability in women aged 20 to 80 years. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 58,* M525-M530.

Connelly, S. L. & Hasher, L. (1993). Aging and the inhibition of spatial location. *Journal of experimental psychology: Human perception and performance, 19,* 1238.

Crossland, M. D., Morland, A. B., Feely, M. P., von dem Hagen, E., & Rubin, G. S. (2008). The effect of age and fixation instability on retinotopic mapping of primary visual cortex. *Investigative Ophthalmology & Visual Science, 49,* 3734-3739.

Cuisinier, R., Olivier, I., Vaugoyeau, M., Nougier, V., & Assaiante, C. (2011). Reweighting of sensory inputs to control quiet standing in children from 7 to 11 and in adults. *PloS one, 6,* e19697.

Cullen, K. E., Brooks, J. X., Jamali, M., Carriot, J., & Massot, C. (2011). Internal models of self-motion: computations that suppress vestibular reafference in early vestibular processing. *Experimental brain research, 210,* 377-388.

de Boer, M. R., Pluijm, S. M., Lips, P., Moll, A. C., Völker-Dieben, H. J., Deeg, D. J. et al. (2004). Different aspects of visual impairment as risk factors for falls and fractures in older men and women. *Journal of bone and Mineral Research, 19,* 1539-1547.

De Smet, K., Malcolm, P., Lenoir, M., Segers, V., & De Clercq, D. (2009). Effects of optic flow on spontaneous overground walk-to-run transition. *Experimental brain research, 193,* 501-508.

De Vignemont, F. (2010). Body schema and body image - Pros and cons. *Neuropsychologia, 48,* 669-680.

Della Santina, C. C., Potyagaylo, V., Migliaccio, A. A., Minor, L. B., & Carey, J. P. (2005). Orientation of human semicircular canals measured by three-dimensional multiplanar CT reconstruction. *Journal of the Association for Research in Otolaryngology, 6,* 191-206.

Deshpande, N. & Patla, A. E. (2005). Dynamic visual-vestibular integration during goal directed human locomotion. *Experimental brain research, 166,* 237-247.

Deutschländer, A., Bense, S., Stephan, T., Schwaiger, M., Brandt, T., & Dieterich, M. (2002). Sensory system interactions during simultaneous vestibular and visual stimulation in PET. *Human brain mapping, 16,* 92-103.

Di Fabio, R. P. (2001). Suppression of the vertical vestibulo-ocular reflex in older persons at risk of falling. *Acta Oto-Laryngologica, 121,* 707-714.

Dichgans, J., Held, R., Young, L. R., & Brandt, T. (1972). Moving visual scenes influence the apparent direction of gravity. *Science, 178,* 1217-1219.

Doumas, M. & Krampe, R. T. (2010). Adaptation and reintegration of proprioceptive information in young and older adults' postural control. *Journal of neurophysiology, 104,* 1969.

Du Pasquier, R. A., Blanc, Y., Sinnreich, M., Landis, T., Burkhard, P., & Vingerhoets, F. J. G. (2003). The effect of aging on postural stability: a cross sectional and longitudinal study. *Neurophysiologie Clinique/Clinical Neurophysiology, 33,* 213-218.

Dustman, R. E., Emmerson, R. Y., & Shearer, D. E. (1996). Life span changes in electrophysiological measures of inhibition. *Brain and cognition, 30,* 109-126.

Edwards, J. D., Ross, L. A., Wadley, V. G., Clay, O. J., Crowe, M., Roenker, D. L. et al. (2006). The useful field of view test: Normative data for older adults. *Archives of Clinical Neuropsychology, 21,* 275-286.

Edwards, J. D., Vance, D. E., Wadley, V. G., Cissell, G. M., Roenker, D. L., & Ball, K. K. (2005). Reliability and validity of useful field of view test scores as administered by personal computer. *Journal of clinical and experimental neuropsychology, 27,* 529-543.

Eikema, D. J., Hatzitaki, V., Konstantakos, V., & Papaxanthis, C. (2013). Elderly adults delay proprioceptive reweighting during the anticipation of collision avoidance when standing. *Neuroscience, 234,* 22-30.

Eikema, D. J., Hatzitaki, V., Tzovaras, D., & Papaxanthis, C. (2012). Age-dependent modulation of sensory reweighting for controlling posture in a dynamic virtual environment. *AGE, 34,* 1381-1392.

Emerson, J. L., Johnson, A. M., Dawson, J. D., Uc, E. Y., Anderson, S. W., & Rizzo, M. (2012). Predictors of Driving Outcomes in Advancing Age. *Psychology and aging, 27,* 550-559.

Ernst, M. O. & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415,* 429-433.

Ernst, M. O. & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8,* 162-169.

Faraldo-Garcia, A., Santos-Pérez, S., Crujeiras-Casais, R., Labella-Caballero, T., & Soto-Varela, A. (2012). Influence of age and gender in the sensory analysis of balance control. *European Archives of Oto-Rhino-Laryngology, 269,* 673-677.

Flückiger, M. & Baumberger, B. (1988). The perception of an optical flow projected on the ground surface. *Perception, 17,* 633.

Forssberg, H. & Nashner, L. M. (1982). Ontogenetic development of postural control in man: adaptation to altered support and visual conditions during stance. *The Journal of Neuroscience, 2,* 545-552.

Fourre, B., Isableu, B., Bernardin, D., Gueguen, M., Giraudet, G., Vuillerme, N. et al. (2009). The role of body centre of mass on haptic subjective vertical. *Neurosci Lett., 465,* 230-234.

François, M., Morice, A. H., Bootsma, R. J., & Montagne, G. (2011). Visual control of walking velocity. *Neuroscience research, 70,* 214-219.

Franz, J. R., Francis, C. A., Allen, M. S., O'Connor, S. M., & Thelen, D. G. (2015). Advanced age brings a greater reliance on visual feedback to maintain balance during walking. *Human Movement Science, 40,* 381-392.

Freeman, E. E., Munoz, B., Rubin, G., & West, S. K. (2007). Visual field loss increases the risk of falls in older adults: the Salisbury eye evaluation. *Investigative Ophthalmology & Visual Science, 48,* 4445-4450.

Fukuda, T. (1959). The stepping test: two phases of the labyrinthine reflex. *Acta Oto-Laryngologica, 50,* 95.

Funk, J., Finke, K., Müller, H. J., Utz, K. S., & Kerkhoff, G. (2011). Visual context modulates the subjective vertical in neglect: evidence for an increased rod-and-frame-effect. *Neuroscience, 173,* 124-134.

Gauchard, G., Jeandel, C., & Perrin, P. P. (2001). Physical and sporting activities improve vestibular afferent usage and balance in elderly human subjects. *Gerontology, 47,* 263-270.

Gibson, J. J. (1950). The perception of visual surfaces. *The American journal of psychology,* 367-384.

Goble, D. J. (2009). Proprioceptive sensibility in the elderly: degeneration, functional consequences and plastic-adaptive processes.

Goble, D. J. (2010). Proprioceptive acuity assessment via joint position matching: from basic science to general practice. *Physical Therapy, 90,* 1176-1184.

Goble, D. J. (2011). Brain activity during ankle proprioceptive stimulation predicts balance performance in young and older adults.

Good, C. D., Johnsrude, I. S., Ashburner, J., Henson, R. N., Friston, K. J., & Frackowiak, R. S. (2001). A voxel-based morphometric study of ageing in 465 normal adult human brains. *NeuroImage, 14,* 21-36.

Goode, K., Ball, K., Sloane, M., Roenker, D., Roth, D., Myers, R. et al. (1998). Useful Field of View and Other Neurocognitive Indicators of Crash Risk in Older Adults. *Journal of Clinical Psychology in Medical Settings, 5,* 425-440.

Goodenough, D. R., Oltman, P. K., & Cox, P. W. (1987). The nature of individual differences in field dependence. *Journal of Research in Personality, 21,* 81-99.

Grasso, R., Assaiante, C., Prévost, P., & Berthoz, A. (1998). Development of Anticipatory Orienting Strategies During Locomotor Tasks in Children. *Neuroscience & Biobehavioral Reviews, 22,* 533-539.

Gueguen, M., Vuillerme, N., & Isableu, B. (2012). Does the integration of haptic and visual cues reduce the effect of a biased visual reference frame on the subjective head orientation? *PLoS.One., 7,* e34380.

Guerraz, M. & Bronstein, A. M. (2008). Ocular versus extraocular control of posture and equilibrium. *Neurophysiologie Clinique/Clinical Neurophysiology, 38,* 391-398.

Guerraz, M., Luyat, M., Poquin, D., & Ohlmann, T. (2000). The role of neck afferents in subjective orientation in the visual and tactile sensory modalities. *Acta Otolaryngol., 120,* 735-738.

Guerraz, M., Poquin, D., Luyat, M., & Ohlmann, T. (1998). Head orientation involvement in assessment of the subjective vertical during whole body tilt. *Percept.Mot.Skills, 87,* 643-648.

Guerraz, M., Poquin, D., & Ohlmann, T. (1998). The role of head-centric spatial reference with a static and kinetic visual disturbance. *Percept.Psychophys., 60,* 287-295.

Guerraz, M., Yardley, L., Bertholon, P., Pollak, L., Rudge, P., Gresty, M. A. et al. (2001). Visual vertigo: symptom assessment, spatial orientation and postural control. *Brain, 124,* 1646-1656.

Guerrier, J. H., Manivannan, P., & Nair, S. N. (1999). The role of working memory, field dependence, visual search, and reaction time in the left turn performance of older female drivers. *Applied Ergonomics, 30,* 109-119.

Gurfinkel, V. S., Ivanenko, Y. P., Levik, Y. S., & Babakova, I. A. (1995). Kinesthetic reference for human orthograde posture. *Neuroscience, 68,* 229-243.

Haas, A., Flammer, J., & Schneider, U. (1986). Influence of age on the visual fields of normal subjects. *American journal of ophthalmology, 101,* 199-203.

Harrison, S. J. & Stergiou, N. (2015). Complex Adaptive Behavior and Dexterous Action. *Nonlinear dynamics, psychology, and life sciences, 19,* 345-394.

Hay, L., Bard, C., Fleury, M., & Teasdale, N. (1996). Availability of visual and proprioceptive afferent messages and postural control in elderly adults. *Exp Brain Res, 108,* 129-139.

Haywood, K., Teeple, J., Givens, M., & Patterson, J. (1977). Young children's rod-and-frame test performance. *Perceptual and motor skills, 45,* 163-169.

Hedden, T. & Gabrieli, J. D. E. (2004). Insights into the ageing mind: a view from cognitive neuroscience. *Nat Rev Neurosci, 5,* 87-96.

Herishanu, Y. O. & Sharpe, J. A. (1981). Normal square wave jerks. *Investigative Ophthalmology & Visual Science, 20,* 268-272.

Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R., & Swinnen, S. P. (2005). Neural basis of aging: the penetration of cognition into action control. *The Journal of Neuroscience, 25,* 6787-6796.

Heuninckx, S., Wenderoth, N., & Swinnen, S. P. (2008). Systems neuroplasticity in the aging brain: recruiting additional neural resources for successful motor performance in elderly persons. *The Journal of Neuroscience, 28,* 91-99.

Hirasaki, E., Kubo, T., Nozawa, S., Matano, S., & Matsunaga, T. (1993). Analysis of head and body movements of elderly people during locomotion. *Acta Oto-Laryngologica, 113,* 25-30.

Hotson, J. R. & Steinke, G. W. (1988). Vertical and horizontal saccades in aging and dementia: failure to inhibit anticipatory saccades. *Neuro-ophthalmology, 8,* 267-273.

Hurley, M. V., Rees, J., & Newham, D. J. (1998). Quadriceps function, proprioceptive acuity and functional performance in healthy young, middle-aged and elderly subjects. *Age and Ageing, 27,* 55-62.

Isableu, B., Fourre, B., Vuillerme, N., Giraudet, G., & Amorim, M. A. (2011). Differential integration of visual and kinaesthetic signals to upright stance. *Exp Brain Res, 212,* 33-46.

Isableu, B., Ohlmann, T., Crémieux, J., & Amblard, B. (1997). Selection of spatial frame of reference and postural control variability. *Exp Brain Res, 114,* 584-589.

Isableu, B., Ohlmann, T., Crémieux, J., Vuillerme, N., Amblard, B., & Gresty, M. A. (2010). Individual differences in the ability to identify, select and use appropriate frames of reference for perceptuo-motor control. *Neuroscience, 169,* 1199-1215.

Isableu, B., Rezzoug, N., Mallet, G., Bernardin, D., Gorce, P., & Pagano, C. C. (2009). Velocity-dependent changes of rotational axes in the non-visual control of unconstrained 3D arm motions. *Neuroscience, 164,* 1632-1647.

Isableu, B. & Vuillerme, N. (2006). Differential integration of kinaesthetic signals to postural control. *Exp Brain Res, 174,* 763-768.

Isableu, B., Ohlmann, T., Crémieux, J., & Amblard, B. (1998). How dynamic visual field dependence-independence interacts with the visual contribution to postural control. *Human Movement Science, 17,* 367-391.

Isableu, B., Ohlmann, T., Crémieux, J., & Amblard, B. (2003). Differential approach to strategies of segmental stabilisation in postural control. *Exp Brain Res, 150,* 208-221.

Itoh, N. & Fukuda, T. (2002). Comparative study of eye movements in extent of central and peripheral vision and use by young and elderly walkers. *Perceptual and motor skills, 94,* 1283-1291.

Ivry, R. B., Spencer, R. M., Zelaznik, H. N., & Diedrichsen, J. +. (2002). The cerebellum and event timing. *Annals of the New York Academy of Sciences, 978,* 302-317.

Jaffe, G. J., Alvarado, J. A., & Juster, R. P. (1986). Age-Related Changes of the Normal Visual Field. *Archives of Ophthalmology, 104,* 1021.

Jahn, K., Deutschländer, A., Stephan, T., Strupp, M., Wiesmann, M., & Brandt, T. (2004). Brain activation patterns during imagined stance and locomotion in functional magnetic resonance imaging. *NeuroImage, 22,* 1722-1731.

Jahn, K., Strupp, M., Schneider, E., Dieterich, M., & Brandt, T. (2001). Visually induced gait deviations during different locomotion speeds. *Experimental brain research, 141,* 370-374.

Jamet, M., Deviterne, D., Gauchard, G. C., Vancon, G., & Perrin, P. P. (2004). Higher visual dependency increases balance control perturbation during cognitive task fulfilment in elderly people. *Neurosci.Lett., 359,* 61-64.

Jamet, M., Deviterne, D., Gauchard, G. C., Vancon, G., & Perrin, P. P. (2007). Age-related part taken by attentional cognitive processes in standing postural control in a dual-task context. *Gait Posture, 25,* 179-184.

Jeeves, M. A. & Moes, P. (1996). Interhemispheric transfer time differences related to aging and gender. *Neuropsychologia, 34,* 627-636.

Jeka, J., Allison, L., Saffer, M., Zhang, Y., Carver, S., & Kiemel, T. (2006). Sensory reweighting with translational visual stimuli in young and elderly adults: the role of state-dependent noise. *Exp Brain Res, 174,* 517-527.

Jeka, J. J. A. (2010). The Dynamics of Visual Reweighting in Healthy and Fall-Prone Older Adults. *Journal of Motor Behavior, 42,* 197-208.

Jernigan, T. L., Archibald, S. L., Fennema-Notestine, C., Gamst, A. C., Stout, J. C., Bonner, J. et al. (2001). Effects of age on tissues and regions of the cerebrum and cerebellum. *Neurobiology of Aging, 22,* 581-594.

Judge, J. O., King, M. B., Whipple, R., & Clive, J. (1995). Dynamic balance in older persons: effects of reduced visual and proprioceptive input. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 50,* M263-M270.

Kang, H. G. & Dingwell, J. B. (2008). Effects of walking speed, strength and range of motion on gait stability in healthy older adults. *Journal of biomechanics, 41,* 2899-2905.

Kapoula, Z. & Lê, T. T. (2006). Effects of distance and gaze position on postural stability in young and old subjects. *Experimental brain research, 173,* 438-445.

Kaptein, R. G. & Van Gisbergen, J. A. (2004). Interpretation of a discontinuity in the sense of verticality at large body tilt. *Journal of neurophysiology, 91,* 2205-2214.

Karp, S. A. (1967). Field dependence and occupational activity in the aged. *Perceptual and motor skills, 24,* 603-609.

Kavounoudias, A., Gilhodes, J. C., Roll, R. +., & Roll, J. P. (1999). From balance regulation to body orientation: two goals for muscle proprioceptive information processing? *Experimental brain research, 124,* 80-88.

Keshner, E. A. (2004). Head-trunk coordination in elderly subjects during linear anterior-posterior translations. *Exp.Brain Res., 158,* 213-222.

Keshner, E. A. & Kenyon, R. V. (2000). The influence of an immersive virtual environment on the segmental organization of postural stabilizing responses. *Journal of Vestibular Research, 10,* 207-220.

Klein, B. E. K., Moss, S. E., Klein, R., Lee, K. E., & Cruickshanks, K. J. (2003). Associations of visual function with physical outcomes and limitations 5 years later in an older population: The Beaver Dam eye study. *Ophthalmology, 110,* 644-650.

Kluzik, J., Horak, F. B., & Peterka, R. J. (2005). Differences in preferred reference frames for postural orientation shown by after-effects of stance on an inclined surface. *Experimental brain research, 162,* 474-489.

Kluzik, J., Peterka, R. J., & Horak, F. B. (2007). Adaptation of postural orientation to changes in surface inclination. *Experimental brain research, 178,* 1-17.

Kobayashi, H., Hayashi, Y., Higashino, K., Saito, A., Kunihiro, T., Kanzaki, J. et al. (2002). Dynamic and static subjective visual vertical with aging. *Auris Nasus Larynx, 29,* 325-328.

Konczak, J. (1994). Effects of optic flow on the kinematics of human gait: a comparison of young and older adults. *Journal of Motor Behavior, 26,* 225-236.

Kosnik, W., Fikre, J., & Sekuler, R. (1986). Visual fixation stability in older adults. *Investigative Ophthalmology & Visual Science, 27,* 1720-1725.

Kosnik, W., Kline, D., Fikre, J., & Sekuler, R. (1987). Ocular fixation control as a function of age and exposure duration. *Psychology and aging, 2,* 302.

Lafargue, G., Noël, M., & Luyat, M. (2013). In the elderly, failure to update internal models leads to over-optimistic predictions about upcoming actions. *PloS one, 8,* e51218.

Lamontagne, A., Fung, J., McFadyen, B. J., & Faubert, J. (2007). Modulation of walking speed by changing optic flow in persons with stroke. *Journal of neuroengineering and rehabilitation, 4,* 22.

Laudani, L., Casabona, A., Perciavalle, V., & Macaluso, A. (2006). Control of head stability during gait initiation in young and older women. *Journal of Electromyography and Kinesiology, 16,* 603-610.

Lee, D. N. & Lishman, J. R. (1975). Visual proprioceptive control of stance. *Journal of human movement studies*.

Lee, J. A. & Pollack, R. H. (1978). The effects of age on perceptual problem-solving strategies. *Experimental aging research, 4,* 37-54.

Lee, J. & Pollack, R. (1980). The effects of age on perceptual field dependence. *Bull.Psychon.Soc., 15,* 239-241.

Legault, I., Allard, R., & Faubert, J. (2013). Healthy older observers show equivalent perceptual-cognitive training benefits to young adults for multiple object tracking. *Frontiers in psychology, 4*.

Lewald, J. & Ehrenstein, W. H. (2000). Visual and proprioceptive shifts in perceived egocentric direction induced by eye-position. *Vision research, 40,* 539-547.

Li, L., Peli, E., & Warren, W. H. (2002). Heading Perception in Patients with Advanced Retinitis Pigmentosa. *Optometry & Vision Science, 79*.

Lindenberger, U., Marsiske, M., & Baltes, P. B. (2000). Memorizing while walking: increase in dual-task costs from young adulthood to old age. *Psychology and aging, 15,* 417.

Liston, M. B., Bamiou, D. E., Martin, F., Hopper, A., Koohi, N., Luxon, L. et al. (2013). Peripheral vestibular dysfunction is prevalent in older adults experiencing multiple non-syncopal falls versus age-matched non-fallers: a pilot study. *Age and Ageing,* aft129.

Liu, W. (2003). Field dependence-independence and sports with a preponderance of closed or open skill. *Journal of Sport Behaviour, 26,* 285-297.

Lopez, C., Lacour, M., El Ahmadi, A., Magnan, J., & Borel, L. (2007). Changes of visual vertical perception: a long-term sign of unilateral and bilateral vestibular loss. *Neuropsychologia, 45,* 2025-2037.

Lord, S. R., Clark, R. D., & Webster, I. W. (1991a). Physiological factors associated with falls in an elderly population. *J.Am.Geriatr.Soc., 39,* 1194-1200.

Lord, S. R., Menz, H. B., & Tiedemann, A. (2003). A physiological profile approach to falls risk assessment and prevention. *Phys.Ther., 83,* 237-252.

Lord, S. R. & Ward, J. A. (1994). Age-associated differences in sensori-motor function and balance in community dwelling women. *Age and Ageing, 23,* 452.

Lord, S. R. & Webster, I. W. (1990). Visual field dependence in elderly fallers and non-fallers. *Int.J.Aging Hum.Dev., 31,* 267-277.

Lord, S., Sherrington, C., & Menz, H. (2005). Ageing and falls. *Understanding and Preventing Falls: An Ergonomics Approach*, 75.

Lord, S. R., Clark, R. D., & Webster, I. W. (1991b). Visual Acuity and Contrast Sensitivity in Relation to Falls in an Elderly Population. *Age and Ageing, 20,* 175-181.

Lord, S. R., Clark, R. D., & Webster, I. W. (1991c). Postural stability and associated physiological factors in a population of aged persons. *Journal of Gerontology, 46,* M69-M76.

Lord, S. R. & Menz, H. B. (2000). Visual contributions to postural stability in older adults. *Gerontology, 46,* 306-310.

Luyat, M., Ohlmann, T. o., & Barraud, P. A. (1997). Subjective vertical and postural activity. *Acta psychologica, 95,* 181-193.

Macedo, A. F., Crossland, M. D., & Rubin, G. S. (2008). The effect of retinal image slip on peripheral visual acuity. *Journal of vision, 8,* 16.

Manchester, D., Woollacott, M., Zederbauer-Hylton, N., & Marin, O. (1989). Visual, Vestibular and Somatosensory Contributions to Balance Control in the Older Adult. *Journal of Gerontology, 44,* M118-M127.

Manckoundia, P., Mourey, F., Pfitzenmeyer, P., Van Hoecke, J., & Pérennou, D. (2007). Is backward disequilibrium in the elderly caused by an abnormal perception of verticality? A pilot study. *Clinical Neurophysiology, 118,* 786-793.

Marendaz, C. (1984). Dépendance-indépendance á l'égard du champ, activités opératoires et sénescence. *L'Année Psychologique, 84,* 185-205.

Marigold, D. S. & Eng, J. J. (2006). The relationship of asymmetric weight-bearing with postural sway and visual reliance in stroke. *Gait & Posture, 23,* 249-255.

Markus, E. J. (1971). Perceptual field dependence among aged persons. *Perceptual and motor skills, 33,* 175-178.

Markus, E. J. & Nielsen, M. (1973). Embedded-figures test scores among five samples of aged persons. *Perceptual and motor skills, 36,* 455-459.

Matas, N. A., Nettelbeck, T., & Burns, N. R. (2014). Cognitive and visual predictors of UFOV performance in older adults. *Accident Analysis & Prevention, 70,* 74-83.

Matheson, A. J., Darlington, C. L., & Smith, P. F. (1998). Age-related changes in human optokinetic function. *Neuroreport, 9,* 2175-2177.

Mathias, J. L. & Lucas, L. K. (2009). Cognitive predictors of unsafe driving in older drivers: a meta-analysis. *International psychogeriatrics, 21,* 637-653.

Maylor, E. A. & Wing, A. M. (1996). Age differences in postural stability are increased by additional cognitive demands. *J.Gerontol.B Psychol.Sci.Soc.Sci., 51,* 143-154.

Mazaheri, M., Hoogkamer, W., Potocanac, Z., Verschueren, S., Roerdink, M., Beek, P. J. et al. (2015). Effects of aging and dual tasking on step adjustments to perturbations in visually cued walking. *Experimental brain research, 233,* 3467-3474.

Mccarley, J. S. & He, Z. J. (2000). Asymmetry in 3-D perceptual organization: Ground-like surface superior to ceiling-like surface. *Perception & psychophysics, 62,* 540-549.

McIntyre, J., Berthoz, A., & Lacquaniti, F. (1998). Reference frames and internal models for visuo-manual coordination: what can we learn from microgravity experiments? *Brain Research Reviews, 28,* 143-154.

McKnight, A. J. & McKnight, A. S. (1999). Multivariate analysis of age-related driver ability and performance deficits. *Accident Analysis & Prevention, 31,* 445-454.

McLeod, B. (1985). Field dependence as a factor in sports with preponderance of open or closed skills. *Perceptual and motor skills, 60,* 369-370.

Merfeld, D. M., Zupan, L., & Peterka, R. J. (1999). Humans use internal models to estimate gravity and linear acceleration. *Nature, 398,* 615-618.

Mergner, T., Schweigart, G., Maurer, C., & Blümle, A. (2005). Human postural responses to motion of real and virtual visual environments under different support base conditions. *Experimental brain research, 167,* 535-556.

Mergner, T. & Rosemeier, T. (1998). Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under terrestrial and microgravity conditions - a conceptual model. *Brain Research Reviews, 28,* 118-135.

Mesure, S., Azulay, J. P., Pouget, J., & Amblard, B. (1999). Strategies of segmental stabilization during gait in Parkinson's disease. *Experimental brain research, 129,* 573-581.

Mihal, W. L. & Barrett, G. V. (1976). Individual differences in perceptual information processing and their relation to automobile accident involvement. *Journal of Applied Psychology, 61,* 229.

Mittelstaedt, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschaften, 70,* 272-281.

Miyai, I., Mauricio, R. L., & Reding, M. J. (1997). Parietal-insular strokes are associated with impaired standing balance as assessed by computerized dynamic posturography. *Neurorehabilitation and Neural Repair, 11,* 35-40.

Mohler, B. J., Thompson, W. B., Creem-Regehr, S. H., Pick Jr, H. L., & Warren Jr, W. H. (2007). Visual flow influences gait transition speed and preferred walking speed. *Experimental brain research, 181,* 221-228.

Morasso, P. & Sanguineti, V. (1995). Self-organizing body schema for motor planning. *Journal of Motor Behavior, 27,* 52-66.

Murakami, I., Kitaoka, A., & Ashida, H. (2006). A positive correlation between fixation instability and the strength of illusory motion in a static display. *Vision research, 46,* 2421-2431.

Nilsson, N. C., Serafin, S., & Nordahl, R. (2014). Establishing the range of perceptually natural visual walking speeds for virtual walking-in-place locomotion. *IEEE transactions on visualization and computer graphics, 20,* 569-578.

O'Connor, K. W., Loughlin, P. J., Redfern, M. S., & Sparto, P. J. (2008). Postural adaptations to repeated optic flow stimulation in older adults. *Gait & Posture, 28,* 385-391.

O'Connor, S. M. & Kuo, A. D. (2009). Direction-dependent control of balance during walking and standing. *Journal of neurophysiology, 102,* 1411-1419.

O'Loughlin, J. L., Robitaille, Y., Boivin, J. F., & Suissa, S. (1993). Incidence of and risk factors for falls and injurious falls among the community-dwelling elderly. *American journal of epidemiology, 137,* 342-354.

Oie, K. S., Kiemel, T., & Jeka, J. J. (2002). Multisensory fusion: simultaneous re-weighting of vision and touch for the control of human posture. *Cognitive Brain Research, 14,* 164-176.

Oltman, P. K. (1968). A portable rod-and-frame apparatus. *Perceptual and motor skills, 26,* 503-506.

Oltman, P. K., Raskin, E., Witkin, H. A., & Press, C. P. (1971). *Group embedded figures test*. Consulting Psychologists Press Palo Alto, CA.

Osaka, N. (1993). Apparent motion in the upper and lower peripheral visual field. *16th ECPV, 22*.

Owsley, C. (2011). Aging and vision. *Vision Res, 51,* 1610-1622.

Owsley, C., Ball, K., McGwin Jr, G., Sloane, M. E., Roenker, D. L., White, M. F. et al. (1998). Visual processing impairment and risk of motor vehicle crash among older adults. *Jama, 279,* 1083-1088.

Owsley, C., Ball, K., Sloane, M. E., Roenker, D. L., & Bruni, J. R. (1991). Visual/cognitive correlates of vehicle accidents in older drivers. *Psychology and aging, 6,* 403.

Pagano, C. C. & Turvey, M. T. (1995). The inertia tensor as a basis for the perception of limb orientation. *Journal of experimental psychology: Human perception and performance, 21,* 1070.

Paige, G. (1994). Senescence of human visual-vestibular interactions: smooth pursuit, optokinetic, and vestibular control of eye movements with aging. *Exp Brain Res, 98,* 355-372.

Pailhous, J., Ferrandez, A. M., Flückiger, M., & Baumberger, B. (1990). Unintentional modulations of human gait by optical flow. *Behavioural brain research, 38,* 275-281.

Paillard, J. (1999). Body Schema and Body Image - A Double Dissociation. *Motor control, today and tomorrow,* 197-214.

Panek, P. E., Barrett, G. V., Sterns, H. L., & Alexander, R. A. (1978). Age differences in perceptual style, selective attention, and perceptual-motor reaction time. *Experimental aging research, 4,* 377-387.

Paquette, M. R. & Vallis, L. A. (2010). Age-related kinematic changes in late visual-cueing during obstacle circumvention. *Experimental brain research, 203,* 563-574.

Pavlou, M., Quinn, C., Murray, K., Spyridakou, C., Faldon, M., & Bronstein, A. M. (2011). The effect of repeated visual motion stimuli on visual dependence and postural control in normal subjects. *Gait & Posture, 33,* 113-118.

Pelak, V. (2010). Ocular Motility of Aging and Dementia. *Curr Neurol Neurosci Rep, 10,* 440-447.

Pelli, D. G., Robson, J. G., & Wilkins, A. J. (1988). The design of a new letter chart for measuring contrast sensitivity. *Clinical Vision Sciences, 2,* 187-199.

Perennou, D. A., Amblard, B., Leblond, C., & Pelissier, J. (1998). Biased postural vertical in humans with hemispheric cerebral lesions. *Neuroscience letters, 252,* 75-78.

Personnier, P., Ballay, Y., & Papaxanthis, C. (2010). Mentally represented motor actions in normal aging: III. Electromyographic features of imagined arm movements. *Behavioural brain research, 206,* 184-191.

Personnier, P., Paizis, C., Ballay, Y., & Papaxanthis, C. (2008). Mentally represented motor actions in normal aging: II. The influence of the gravito-inertial context on the duration of overt and covert arm movements. *Behavioural brain research, 186,* 273-283.

Peterka, R. J. & Loughlin, P. J. (2004). Dynamic regulation of sensorimotor integration in human postural control. *Journal of neurophysiology, 91,* 410-423.

Polcyn, A. F., Lipsitz, L. A., Kerrigan, D. C., & Collins, J. J. (1998). Age-related changes in the initiation of gait: degradation of central mechanisms for momentum generation. *Archives of physical medicine and rehabilitation, 79,* 1582-1589.

Poulain, I., Giraudet, G., & Dobrescu, N. (2004). Age-related changes in perception of verticality with a static or kinetic visual-field disturbance. In.

Poulain, I., Gaignard, C., Marin, G., Mantel, B., & Bernardin, D. (2015). Individual differences in perception and control of walking direction. *Journal of vision, 15,* 1326.

Poulain, I. & Giraudet, G. (2008). Age-related changes of visual contribution in posture control. *Gait & Posture, 27,* 1-7.

Pozzo, T., Berthoz, A., & Lefort, L. (1990). Head stabilization during various locomotor tasks in humans. *Experimental brain research, 82,* 97-106.

Pozzo, T., Berthoz, A., Lefort, L., & Vitte, E. (1991). Head stabilization during various locomotor tasks in humans. II. Patients with bilateral peripheral vestibular deficits. *Experimental brain research, 85,* 208.

Prokop, T., Schubert, M., & Berger, W. (1997). Visual influence on human locomotion modulation to changes in optic flow. *Experimental brain research, 114,* 63-70.

Raz, N., Gunning, F. M., Head, D., Dupuis, J. H., McQuain, J., Briggs, S. D. et al. (1997). Selective aging of the human cerebral cortex observed in vivo: differential vulnerability of the prefrontal gray matter. *Cereb.Cortex, 7,* 268-282.

Raz, N., Gunning-Dixon, F., Head, D., Williamson, A., & Acker, J. D. (2001). Age and sex differences in the cerebellum and the ventral pons: a prospective MR study of healthy adults. *American Journal of Neuroradiology, 22,* 1161-1167.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A. et al. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cerebral cortex, 15,* 1676-1689.

Redfern, M. S., Jennings, J. R., Martin, C., & Furman, J. M. (2001). Attention influences sensory integration for postural control in older adults. *Gait & Posture, 14,* 211-216.

Reed-Jones, J. G., Reed-Jones, R. J., & Hollands, M. A. (2014). Is the size of the useful field of view affected by postural demands associated with standing and stepping? *Neuroscience letters, 566,* 27-31.

Resnick, S. M., Pham, D. L., Kraut, M. A., Zonderman, A. B., & Davatzikos, C. (2003). Longitudinal magnetic resonance imaging studies of older adults: a shrinking brain. *The Journal of Neuroscience, 23,* 3295-3301.

Reuchlin, M. (1978). Processus vicariants et différences individuelles. *Journal de psychologie normale et pathologique, 75,* 133-145.

Richards, E., Bennett, P. J., & Sekuler, A. B. (2006). Age related differences in learning with the useful field of view. *Vision research, 46,* 4217-4231.

Roll, J. P., Vedel, J. P., & Roll, R. (1989). Eye, head and skeletal muscle spindle feedback in the elaboration of body references. *Progress in brain research, 80,* 113.

Roll, J. P. & Roll, R. (1988). From eye to foot: a proprioceptive chain involved in postural control. In B.Amblard, A.Berthoz, & F.Clarac (Eds.), *Posture and Gait: Development, adaptation and modulation.Proceedings of the 9th International Symposium on Postural and gait research* (pp. 155-164). Amsterdam: Elsevier.

Roll, R., Velay, J. L., & Roll, J. P. (1991). Eye and neck proprioceptive messages contribute to the spatial coding of retinal input in visually oriented activities. *Exp Brain Res, 85,* 423-431.

Rosano, C., Rosso, A. L., & Studenski, S. A. (2014). Aging, Brain, and Mobility: Progress and Opportunities. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 69,* 1373-1374.

Rotella, R. J. & Bunker, L. K. (1978). Field dependence and reaction time in senior tennis players (65 and over). *Perceptual and motor skills, 46,* 585-586.

Royden, C. S., Banks, M. S., & Crowell, J. A. (1992). The perception of heading during eye movements. *Nature, 360,* 583-585.

Russell, C., Malhotra, P., Deidda, C., & Husain, M. (2013). Dynamic attentional modulation of vision across space and time after right hemisphere stroke and in ageing. *cortex, 49,* 1874-1883.

Salat, D. H., Buckner, R. L., Snyder, A. Z., Greve, D. N., Desikan, R. S., Busa, E. et al. (2004). Thinning of the cerebral cortex in aging. *Cerebral cortex, 14,* 721-730.

Salthouse, T. A. (2000). Aging and measures of processing speed. *Biological Psychology, 54,* 35-54.

Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging, 30,* 507-514.

Sarre, G., Berard, J., Fung, J., & Lamontagne, A. (2008). Steering behaviour can be modulated by different optic flows during walking. *Neuroscience letters, 436,* 96-101.

Saunders, J. A. & Durgin, F. H. (2011). Adaptation to conflicting visual and physical heading directions during walking. *Journal of vision, 11,* 15.

Schubert, M., Prokop, T., Brocke, F., & Berger, W. (2005). Visual kinesthesia and locomotion in Parkinson's disease. *Movement Disorders, 20,* 141-150.

Schubert, M. C., Tusa, R. J., Grine, L. E., & Herdman, S. J. (2004). Optimizing the Sensitivity of the Head Thrust Test for Identifying Vestibular Hypofunction. *Physical Therapy, 84,* 151-158.

Schwatz, D. W. & Karp, S. A. (1967). Field dependence in a geriatric population. *Perceptual and motor skills, 24,* 495-504.

Scialfa, C. T., Kline, D. W., & Lyman, B. J. (1987). Age differences in target identification as a function of retinal location and noise level: examination of the useful field of view. *Psychology and aging, 2,* 14.

Scialfa, C. T., Thomas, D. M., & Joffe, K. M. (1994). Age differences in the useful field of view: An eye movement analysis. *Optometry & Vision Science, 71,* 736-742.

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T. et al. (2010). Motor control and aging: links to age-related brain structural, functional, and biochemical effects. *Neurosci.Biobehav.Rev., 34,* 721-733.

Sekuler, B., Bennett, P. J., & Mamelak, M. (2000). Effects of Aging on the Useful Field of View. *Experimental aging research, 26,* 103-120.

Sekuler, R. & Ball, K. (1986). Visual localization: Age and practice. *JOSA A, 3,* 864-867.

Shaffer, S. W. & Harrison, A. L. (2007). Aging of the Somatosensory System: A Translational Perspective. *Physical Therapy, 87,* 193-207.

Shallo-Hoffmann, J., Sendler, B., & Mühlendyck, H. (1990). Normal square wave jerks in differing age groups. *Investigative Ophthalmology & Visual Science, 31,* 1649-1652.

Shay, K. A. & Roth, D. L. (1992). Association between aerobic fitness and visuospatial performance in healthy older adults. *Psychology and aging, 7,* 15.

Simoneau, M., Teasdale, N., Bourdin, C., Bard, C., Fleury, M., & Nougier, V. (1999). Aging and postural control: postural perturbations caused by changing the visual anchor. *J.Am.Geriatr.Soc., 47,* 235-240.

Slaboda, J. C., Barton, J. E., Maitin, I. B., & Keshner, E. A. (2009). Visual field dependence influences balance in patients with stroke. *Conf.Proc.IEEE Eng Med.Biol.Soc., 2009,* 1147-1150.

Slaboda, J. C. & Keshner, E. A. (2012). Reorientation to vertical modulated by combined support surface tilt and virtual visual flow in healthy elders and adults with stroke. *J.Neurol., 259,* 2664-2672.

Slaboda, J. C., Lauer, R. T., & Keshner, E. A. (2011). Continuous visual field motion impacts the postural responses of older and younger women during and after support surface tilt. *Exp.Brain Res., 211,* 87-96.

Slaboda, J. C., Lauer, R. T., & Keshner, E. A. (2013). Postural responses of adults with cerebral palsy to combined base of support and visual field rotation. *IEEE Transactions on Neural Systems and Rehabilitation Engineering, 21,* 218-224.

Sloane, P. D., Baloh, R. W., & Honrubia, V. (1989). The vestibular system in the elderly: clinical implications. *American journal of otolaryngology, 10,* 422-429.

Sotirakis, H., Kyvelidou, A., Mademli, L., Stergiou, N., & Hatzitaki, V. (2016). Aging affects postural tracking of complex visual motion cues. *Experimental brain research,* 1-12.

Sparto, P. J., Furman, J. M., & Redfern, M. S. (2006). Head sway response to optic flow: Effect of age is more important than the presence of unilateral vestibular hypofunction. *Journal of vestibular research: equilibrium & orientation, 16,* 137.

Sparto, P. J., Redfern, M. S., Jasko, J. G., Casselbrant, M. L., Mandel, E. M., & Furman, J. M. (2006). The influence of dynamic visual cues for postural control in children aged 7-12 years. *Experimental brain research, 168,* 505-516.

Stelmach, G. E., Teasdale, N., Di Fabio, R. P., & Phillips, J. (1989). Age related decline in postural control mechanisms. *Int.J.Aging Hum.Dev., 29,* 205-223.

Stergiou, N. & Decker, L. M. (2011). Human movement variability, nonlinear dynamics, and pathology: is there a connection? *Human Movement Science, 30,* 869-888.

Straube, A., Botzel, K., Hawken, M., Paulus, W., & Brandt, T. (1988). Postural control in the elderly: differential effects of visual, vestibular and somatosensory input. In B.Amblard, A.Berthoz, & F.Clarac (Eds.), *Posture and Gait: Development, adaptation and modulation.Proceedings of the 9th International Symposium on Postural and gait research* (pp. 105-114).

Streepey, J. W., Kenyon, R. V., & Keshner, E. A. (2007). Visual motion combined with base of support width reveals variable field dependency in healthy young adults. *Exp.Brain Res., 176,* 182-187.

Strupp, M., Glasauer, S., Jahn, K., Schneider, E., Krafczyk, S., & Brandt, T. (2003). Eye movements and balance. *Annals of the New York Academy of Sciences, 1004,* 352-358.

Sundermier, L., Woollacott, M. H., Jensen, J. L., & Moore, S. (1996). Postural Sensitivity to Visual Flow in Aging Adults With and Without Balance Problems. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 51A,* M45-M52.

Sweeney, J. A., Rosano, C., Berman, R. A., & Luna, B. (2001). Inhibitory control of attention declines more than working memory during normal aging. *Neurobiology of Aging, 22,* 39-47.

Teasdale, N. & Simoneau, M. (2001). Attentional demands for postural control: the effects of aging and sensory reintegration. *Gait.Posture., 14,* 203-210.

Teasdale, N., Stelmach, G. E., & Breunig, A. (1991). Postural sway characteristics of the elderly under normal and altered visual and support surface conditions. *J.Gerontol., 46,* B238-B244.

Teasdale, N., Stelmach, G. E., Breunig, A., & Meeuwsen, H. J. (1991). Age differences in visual sensory integration. *Exp Brain Res, 85,* 691-696.

Templeman, J. N., Denbrook, P. S., & Sibert, L. E. (1999). Virtual locomotion: Walking in place through virtual environments. *Presence: teleoperators and virtual environments, 8,* 598-617.

Tinetti, M. E., Speechley, M., & Ginter, S. F. (1988). Risk factors for falls among elderly persons living in the community. *New England journal of medicine, 319,* 1701-1707.

Toebes, M. J., Hoozemans, M. J., Furrer, R., Dekker, J., & van Dieen, J. H. (2012). Local dynamic stability and variability of gait are associated with fall history in elderly subjects. *Gait & Posture, 36,* 527-531.

Van Beuzekom, A. D., Medendorp, W. P., & Van Gisbergen, J. A. M. (2001). The subjective vertical and the sense of self orientation during active body tilt. *Vision research, 41,* 3229-3242.

Varraine, E., Bonnard, M., & Pailhous, J. (2002). Interaction between different sensory cues in the control of human gait. *Experimental brain research, 142,* 374-384.

Vaugoyeau, M., Viel, S., Amblard, B., Azulay, J. P., & Assaiante, C. (2008). Proprioceptive contribution of postural control as assessed from very slow oscillations of the support in healthy humans. *Gait & Posture, 27,* 294-302.

Vaugoyeau, M., Viel, S., Assaiante, C., Amblard, B., & Azulay, J. P. (2007). Impaired vertical postural control and proprioceptive integration deficits in Parkinson's disease. *Neuroscience, 146,* 852-863.

Vaugoyeau, M. & Azulay, J. P. (2010). Role of sensory information in the control of postural orientation in Parkinson's disease. *Journal of the Neurological Sciences, 289,* 66-68.

Verschueren, S. M. P., Brumagne, S., Swinnen, S. P., & Cordo, P. J. (2002). The effect of aging on dynamic position sense at the ankle. *Behavioural brain research, 136,* 593-603.

Viel, S., Vaugoyeau, M., & Assaiante, C. (2010). Postural adaptation of the spatial reference frames to microgravity: back to the egocentric reference frame. *PloS one, 5,* e10259.

Viel, S., Vaugoyeau, M., & Assaiante, C. (2009). Adolescence: a transient period of proprioceptive neglect in sensory integration of postural control. *Motor Control, 13,* 25-42.

Vuillerme, N., Teasdale, N., & Nougier, V. (2001). The effect of expertise in gymnastics on proprioceptive sensory integration in human subjects. *Neuroscience letters, 311,* 73-76.

Wachtel, P. L. (1972). Field dependence and psychological differentiation: Reexamination. *Perceptual and motor skills, 35,* 179-189.

Wade, M. G., Lindquist, R., Taylor, J. R., & Treat-Jacobson, D. (1995). Optical flow, spatial orientation, and the control of posture in the elderly. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 50,* 51-54.

Warren, W. H., Blackwell, A. W., & Morris, M. W. (1989). Age differences in perceiving the direction of self-motion from optical flow. *Journal of Gerontology, 44,* 147-153.

Warren, W. H., Kay, B. A., Zosh, W. D., Duchon, A. P., & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature neuroscience, 4,* 213-216.

Warren, W. H., Morris, M. W., & Kalish, M. (1988). Perception of translational heading from optical flow. *Journal of experimental psychology: Human perception and performance, 14,* 646.

Weber, K. D., Fletcher, W. A., Gordon, C. R., Jones, G. M., & Block, E. W. (1998). Motor learning in the "podokinetic" system and its role in spatial orientation during locomotion. *Experimental brain research, 120,* 377-385.

Winter, D. A. (1995). Human balance and posture control during standing and walking. *Gait & Posture, 3,* 193-214.

Witkin, H. A., Dyk, R. B., Faterson, H. F., Goodenough, D. R., & Karp, S. A. (1962). *Psychological Differentiation: Studies of development*. New York: Wiley.

Witkin, H. A. & Asch, S. E. (1948). Studies in space orientation. IV. Further experiments on perception of the upright with displaced visual fields. *Journal of experimental psychology, 38,* 762.

Witkin, H. A., Goodenough, D. R., & Karp, S. A. (1967). Stability of cognitive style from childhood to young adulthood. *Journal of personality and social psychology, 7*, 291.

Witkin, H. A., Lewis, H. B., Hertzman, M., Machover, K., Meissner, P. B., & Wapner, S. (1954a). *Personality through perception: an experimental and clinical study*. Westport, Connecticut: Greenwood Press.

Witkin, H. A., Lewis, H. B., Hertzman, M., Machover, K., Meissner, P. B., & Wapner, S. (1954b). Personality through perception: an experimental and clinical study.

Witkin, H. A., Oltman, P. K., Raskin, E., & Karp, S. A. (1971). *Manual for embedded figures test, children's embedded figures test, and group embedded figures test*. Palo Alto: CA: Consulting Psychologists Press.

Wolsley, C. J., Sakellari, V., & Bronstein, A. M. (1996). Reorientation of visually evoked postural responses by different eye-in-orbit and head-on-trunk angular positions. *Experimental brain research, 111*, 283-288.

Wood, J. M., Chaparro, A., Lacherez, P., & Hickson, L. (2012). Useful Field of View Predicts Driving in the Presence of Distracters. *Optometry & Vision Science, 89*.

Wood, J. M. & Owsley, C. (2013). Useful field of view test. *Gerontology, 60,* 315-318.

Woollacott, M. H. (1993). 8 Age-Related Changes in Posture and Movement. *Journal of Gerontology, 48,* 56-60.

World Health Organisation. (2015). Ageing and health. Retrieved online: http://www.who.int/mediacentre/factsheets/fs404/en/ [Fact sheet].

Wright, R. L., Peters, D. M., Robinson, P. D., Sitch, A. J., Watt, T. N., & Hollands, M. A. (2012). Differences in axial segment reorientation during standing turns predict multiple falls in older adults. *Gait & Posture, 36,* 541-545.

Wrisley, D. M. & Kumar, N. A. (2010). Functional gait assessment: concurrent, discriminative, and predictive validity in community-dwelling older adults. *Physical Therapy*.

Yan, J. H. (2010). Cognitive styles affect choice response time and accuracy. *Personality and Individual Differences, 48,* 747-751.

Yardley, L. (1990). Contribution of somatosensory information to perception of the visual vertical with body tilt and rotating visual field. *Perception & psychophysics, 48,* 131-134.

Yeh, T. T., Cluff, T., & Balasubramaniam, R. (2014). Visual reliance for balance control in older adults persists when visual information is disrupted by artificial feedback delays. *PloS one, 9,* e91554.

Young, W. R. & Hollands, M. A. (2012). Evidence for age-related decline in visuomotor function and reactive stepping adjustments. *Gait & Posture, 36,* 477-481.

Zietz, D. & Hollands, M. (2009). Gaze behavior of young and older adults during stair walking. *Journal of Motor Behavior, 41,* 357-366.

Zoccolotti, P., Antonucci, G., & Spinelli, D. (1993). The gap between rod and frame influences the rod-and-frame effect with small and large inducing displays. *Perception & psychophysics, 54,* 14-19.

université PARIS-SACLAY | ÉCOLE DOCTORALE Sciences du sport, de la motricité et du mouvement humain (SSMMH)

Title : Reliance on the visual frame of reference in aging across different sensorimotor tasks: from perception to walking

Keywords : aging, frames of reference, visual field dependence, posture, walking, optic flow

Abstract: Aging entails deficits in the mechanisms of sensory integration which may affect daily living tasks in old adults, ultimately leading to loss of autonomy and health risks, notably falls. Among the factors contributing to these risks, some may be associated with a degradation in sensory (re)weighting, leading to a greater reliance on visual cues and the associated frames of reference (FoR) (visual field dependence).

Our aim was to study how preferential modes of spatial referencing influence sensorimotor control. Examining visual field dependence in the context of aging thus allows to better understand:

- if age-related cognition and/or sensorimotor deficits are associated with increased reliance on the visual FoR;
- whether this reliance indicates a preferred mode of spatial referencing or a consequence of age-related deficits;
- how the above associations and mechanisms evolve by studying young, middle-aged and old adults.

We first examined possible factors associated with greater reliance on the visual FoR with age (Chapter 2). We confirmed classic literature reports of increased visual field dependence in old age, and uncovered an association between greater visual field dependence and reduced i) reliance on the egocentric FoR, ii) parallel attentional visual processing ability, and iii) visual fixation stability.

We subsequently examined the orientation and stabilisation behaviour of our participants during postural tasks and while walking under different conditions of linear ground optic flow. In Chapter 3, participants stood quietly or stepped in place (SIP – intermittent podal contacts with the ground surface) while confronted with 1- natural optic flow (no stimulus), 2- a static visual stimulation, 3- approaching and 4- receding optic flow. The results showed that the optic flow stimuli influenced SIP primarily as evidenced by anteroposterior drifting of the head, trunk and centre of pressure (COP). Old adults had larger amplitudes of drift compared to the younger participants, and drifted even under natural flow (natural drift) during SIP, indicating reduced egocentric self-motion perception. The most important *directional* optic flow effects were on the COP and were associated with i) increased reliance on the visual FOR, ii) reduced reliance on the egocentric FoR, and iii) greater natural drift.

In Chapter 4 we investigated the influence of ground optic flow on the control of walking and head stabilisation. Reliance on the visual FoR in old adults was manifested under conditions of i) natural flow by a reduced head pitch orientation and ability to stabilise their head in space, which may indicate a strategy to maximise the salience of available visual cues and ii) imposed optic flow, by a re-orientation of the trunk in pitch and increase in stepping frequency. Our results also revealed a general improvement of head stabilisation under conditions of imposed visual stimulation towards a more frequent adoption of the head stabilisation in space strategy. This suggests that the artificial enhancement of optic flow provokes a postural adaptation in order to optimise sensory information processing when walking.

Our findings extend current knowledge on the association between reliance on the visual FoR and sensorimotor control across adulthood and depending on the perceptivo-motor task. It is evident that this reliance is linked to a reduction in the exploitation of the egocentric FoR in terms of body orientation and self-motion perception, and that its manifestation depends on the task. Finally, our work provides insights for the design of training protocols aimed at frailer olds taking into account exacerbated reliance on the visual FoR.

Titre : Dépendance au cadre de référence visuel au cours du vieillissement en fonction de différentes tâches sensorimotrices: de la perception à la marche

Mots clés : vieillissement, cadres de référence, dépendance à l'égard du champ visuel, posture, marche, flux optique

Résumé : Le vieillissement entraîne une dégradation des mécanismes sensoriels d'intégration pouvant se manifester dans les tâches de la vie quotidienne des seniors par une perte d'autonomie et des risques de chute. Parmi les facteurs contribuant à l'augmentation de ces risques, certains pourraient relever d'une dégradation de la (re)pondération des signaux sensoriels se traduisant par une augmentation de la dépendance aux informations visuelles et aux références spatiales associées.

Examiner la dépendance au référentiel visuel (DRV) dans le contexte du vieillissement permet ainsi de mieux comprendre:

- si des effets d'âge sur la cognition et/ou la sensorimotricité sont liés à l'augmentation de la DRV;
- si la DRV majorée des seniors indique un mode préféré de référentiation spatiale ou une conséquence des déficits liés à l'âge;
- l'évolution de ces associations et ces mécanismes en étudiant des jeunes adultes, des adultes d'âge intermédiaire et des seniors.

Dans le Chapitre 2, nous avons examiné les facteurs associés à une plus grande DRV avec l'âge. Nous avons confirmé les résultats classiques de la littérature en montrant une augmentation de la DRV avec l'âge, de plus celle-ci était associée avec une réduction de i) l'effet Aubert, indiquant une réduction de la dépendance au référentiel égocentré (DRE), ii) la capacité de traitement d'attention visuelle parallèle, et iii) la stabilité de fixation visuelle.

Nous avons étudié ensuite les comportements d'orientation et de stabilisation de nos participants pendant des tâches posturales, et de marche face à des flux optiques linéaires projetés au sol. Dans le Chapitre 3, nos participants se tenaient 1) en posture érigée pieds serrés ou 2) marchaient sur place (MSP - contacts podaux intermittents) face à 1- une stimulation visuelle statique, 2- un flux optique naturel (aucune stimulation), 3- en approche ou 4- en recul. Les flux optiques ont surtout influencé la MSP induisant des dérives antéroposterieures de la tête, du tronc et du centre de pression (CdP). Les dérives étaient plus marquées chez les seniors par rapport aux autres groupes. Ces participants ont aussi montré des dérives naturelles en condition de MSP, i.e. sans stimulation visuelle projetée. La direction du flux optique a provoqué les effets les plus importants sur la dérive du CdP en association avec i) une DRV supérieure, ii) une DRE réduite et iii) une plus grande dérive naturelle,

Dans le chapitre 4, nous avons étudié l'influence de ces mêmes flux sur le contrôle des paramètres de la marche et sur la stabilisation de la tête au cours de la marche. La dépendance au cadre de référence visuel s'est manifestée chez les seniors dans les conditions de i) flux naturel par une stratégie d'abaissement de la tête et une capacité réduite de stabilisation de la tête sur l'espace dont on peut penser que ces comportements visaient à maximiser l'utilisation des indices visuels disponibles, et ii) flux visuels imposés, par une réorientation du tronc et une augmentation de la fréquence du pas. Les résultats montrent aussi une adoption plus fréquente de la stratégie de stabilisation de la tête sur l'espace en conditions imposées de stimulation visuelle. Ce résultat suggère qu'un renforcement artificiel du flux optique mène à une adaptation posturale permettant une meilleure intégration des informations sensorielles pendant la marche.

Nos résultats complètent les connaissances actuelles sur les relations entre la DRV et le contrôle sensorimoteur en fonction de la tâche perceptivo- motrice avec l'âge. Cette dépendance semble être associée à une réduction de l'exploitation du cadre de référence égocentrée en termes de perception de l'orientation du corps/verticale et de mouvement- propre, et se manifeste différemment selon la tâche. Enfin, notre travail ouvre des pistes de réflexion pour tenir compte de la DRV exacerbée dans la conception de protocoles d'entraînement pour des seniors plus dépendants.