

Aging affects the ability to use optic flow in the control of heading during locomotion

Jessica R. Berard · Joyce Fung ·
Bradford J. McFadyen · Anouk Lamontagne

Received: 25 August 2008 / Accepted: 5 December 2008 / Published online: 13 January 2009
© Springer-Verlag 2008

Abstract Perceived self-motion from optic flow is implicated in the control of locomotion. Aging, which affects visual perception and sensorimotor integration, may result in an inability to use optic flow to guide heading while walking. The purpose of this study was to examine whether advanced age could impact on the steering of locomotion, when changing optic flow directions were presented in an immersive virtual environment (VE). Nine young adults (21.56 ± 3.20 years) and nine older adults (66.11 ± 3.95 years) participated in the study. Subjects were asked to walk while viewing a VE through a head-mounted display unit (Kaiser). The VE viewed by the subjects was a large room displayed as an expanding translational optic flow, with the focus of expansion (FOE) located at neutral, 20° or 40° to the right or left. Their task was to walk straight with respect to the VE. Kinematic data in 3D were collected, from which the body's centre of mass (CoM) position and heading direction were calculated. Young subjects were

able to make proper heading adjustments in the VE, with respect to FOE shifts, but not older individuals. Young subjects altered their CoM trajectory so that it was oriented in the direction opposite to the FOE in the physical environment and resulted in small deviation in the VE. The older adults did not adjust their locomotor patterns in response to the different flows presented and maintained similar walking trajectories across all trials. Advanced age results in an altered control of steering of locomotion in response to changing directions of optic flow. This may be related to an impaired perception and/or use of the optic flow, or due to inherent problems in sensorimotor integration.

Keywords Vision · Steering · Walking · Posture · Gait · Orientation · Older adults

Introduction

Optic flow has been shown to be a strong visual cue that provides information about our heading direction (Gibson 1966). Understanding how we use optic flow to guide locomotion may provide valuable information that can be applied to special populations such as the elderly, who are known to have altered steering strategies (Paquette et al. 2008). The increased occurrence of falls in the elderly has been well documented. It is estimated that 18% of falls occur while turning (Nevitt and Cummings 1994), and that falls occurring during a turn are almost eight times more likely to lead to a hip fracture than falling during forward walking (Lipsitz et al. 1991). Despite these alarming statistics, we have yet to determine precisely which factors lead to falls. Declining visual capacity, specifically decreased contrast sensitivity and impaired depth perception, have been associated with an increased risk of falls (Lord 2006).

J. R. Berard · J. Fung · A. Lamontagne (✉)
School of Physical and Occupational Therapy, McGill University,
3654 Prom Sir-William-Osler, Montreal, QC, Canada, H3G 1Y5
e-mail: anouk.lamontagne@mcgill.ca

J. R. Berard
e-mail: jessica.berard@mail.mcgill.ca

J. R. Berard · J. Fung · A. Lamontagne
Jewish Rehabilitation Hospital (CRIR) Research Center,
3205 Place Alton-Goldbloom, Laval, QC, Canada, H7V 1R2

B. J. McFadyen
Quebec Rehabilitation Research Institute (CIRRI),
525 Hamel, Quebec, QC, Canada, G1M 2S8

B. J. McFadyen
Département de Réadaptation, Faculté de Médecine,
Pavillon Ferdinand-Vandry, Université Laval,
Quebec, QC, Canada, G1K 7P4

Given that vision has been shown to be a strong sensory cue for balance and posture, it is reasonable to speculate that the increase in falls and other mobility issues in the elderly may be related to the use of visual motion and optic flow. The reasons for this are twofold: older adults have difficulty integrating multi-sensory information appropriately during a complex task, and may in fact be overly dependent on visual cues (Lord and Webster 1990; Lord 2006; Paquette et al. 2006; Bugnariu and Fung 2007). Secondly, older adults have poorer perceptions of moving visual stimuli. Warren Jr et al. (1989) demonstrated that older adults showed a diminished ability to judge heading direction when presented with optic flow patterns as compared to younger adults. It has also been demonstrated that older adults score significantly worse when performing a motion-defined perceptual task (Norman et al. 2000), and they have also been reported to have less accurate judgements of vehicular speeds (Scialfa et al. 1991; Schiff et al. 1992). Others have reported that older adults have difficulty adapting to distorted vision while walking (Huitema et al. 2005). To date, little is known about how older adults use optic flow during a dynamic task. The aim of this study was to investigate and compare the abilities of young and older adults to use optic flow cues to guide locomotion and heading direction.

Methods

Subjects

Nine healthy young subjects (mean age 21.55 ± 3.20 years) and nine healthy older adults (mean age

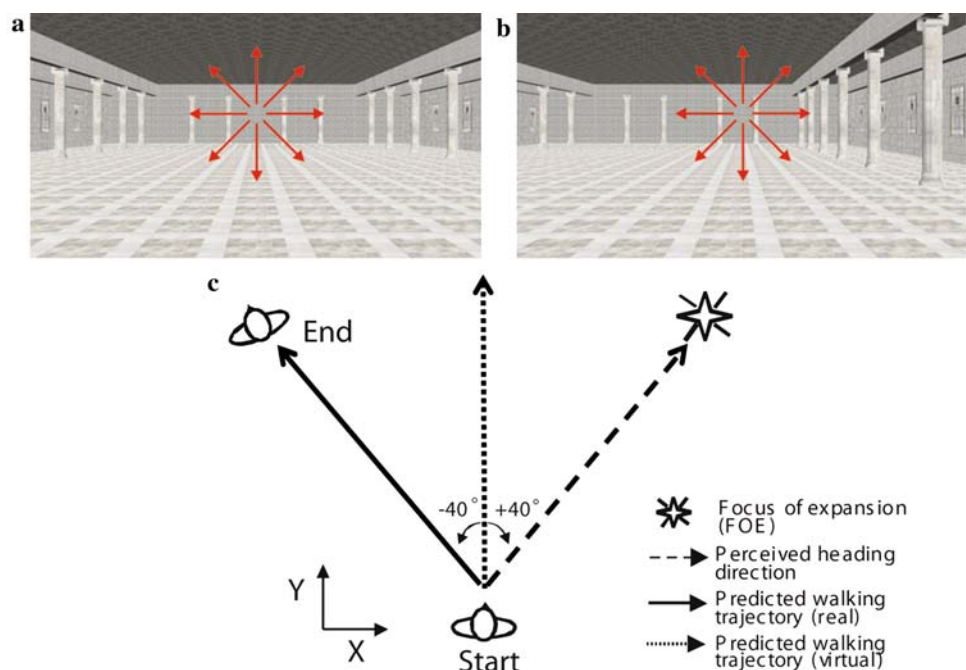
66.11 ± 3.95 years) participated in the study. All participants in the study were naïve to the experiment and had no prior experience moving in virtual environments (VEs). No self-reported musculoskeletal or neurological impairments interfering with locomotion were reported by any of the participants. Subjects with diabetes, history of dizziness or visual problems not corrected by eyewear, were excluded. All subjects signed an informed consent form which was approved by the institutional ethics review committee.

Experimental set up

Subjects walked overground in a large open space in the laboratory ($12 \text{ m} \times 8 \text{ m}$) while wearing a stereoscopic helmet-mounted display unit (HMD; Kaiser Optics ProView™ XL50) with a 50° diagonal field of view. The scene presented in the HMD was designed in Softimage XSI™ and represented a large open room ($40 \text{ m} \times 25 \text{ m}$) with no obstructions (Fig. 1a, b).

Subjects were outfitted with 39 passive reflective markers on anatomical landmarks and kinematic data of the head and whole-body were captured at 120 Hz with a 10-camera Vicon-512™ system. Movements of the head were tracked real-time via three markers placed on the HMD and used by the computer assisted rehabilitation environments-2 (MOTEK BV) to orient the virtual scene. This allowed for real-time movements of the head to be synchronized and displayed in the HMD. The lag between head movements and changes in the scene was approximately 5 ms, and is not perceptible in this task.

Fig. 1 Image of the virtual scene viewed by participants, illustrating the location of the FOE in the 0° condition (a), or an offset of the FOE 40° to the right (b). The schematic below (c) indicates the predicted behaviour of walking trajectory when the focus of expansion is shifted. If the subject perceives that the FOE is shifted 40° to the right, they will correct for the offset by walking 40° to the left in the physical world. This would yield a straight walking trajectory with respect to the virtual environment



Protocol

Subjects were instructed to ‘walk straight in the virtual world’, i.e. their task was to walk straight with respect to the scene that was displayed in the HMD. As the subjects walked through the room, the focus of expansion (FOE) of the scene was shifted laterally in the frontal plane. The magnitude of and direction of the FOE shifts (θ) were 40° (either left or right), 20° (either left or right) and 0° (no displacement). The amount of medio-lateral (ML) displacement (x) was a function of the forward displacement (y) of the subjects’ head, such that $x = y \tan(\theta)$, such that for each meter of forward displacement, the FOE would be shifted by either 0.364 m (20° condition) or 0.839 m (40° condition). Each condition was randomly presented three times, for a total of 15 trials in the testing session. Before data collection began, subjects were given three to five trials which were not recorded to allow them to familiarize themselves with the task. All subjects indicated that they were comfortable in the VE and appeared to walk normally.

Data analysis

Joint angles and body’s centre of mass (CoM) trajectory were calculated in 3D with the Vicon Plug-In-Gait model using marker positions and anthropometric measurements. Data were exported to Matlab and low-pass filtered at 10 Hz using a dual-pass Butterworth filter. Main outcome variables were calculated as the average value between 4 and 4.5 m of forward walking. If the participant did not reach 4 m, then the last available data point was instead used. Variables calculated included the ML deviation of the CoM trajectory with respect to the physical and VEs, as well as heading orientation in the VE. Heading direction was calculated as the instantaneous angular deviation of the CoM trajectory in the horizontal plane. If one were to walk perfectly straight in the VE as instructed, a virtual heading of 0° would be observed. Heading in the VE was thus used to quantify the heading error. Secondary outcome variables included the orientation of the head, trunk and pelvis in the yaw direction with respect to the physical environment.

Statistical analysis

For each measured variable of each participant, the three trials in each condition were averaged together. A mixed model 2-way repeated measures ANOVA, with age (young vs old) as a between-subject factor and FOE location (40°/20° right vs 0° vs 20°/40° left) as a within-subject factor, was applied to determine their effects on CoM deviation, heading error and segment orientations. Where significant

main or interaction effects existed, Tukey’s post hoc comparisons were used to identify differences between groups. The level of significance was set at $P < 0.05$ and adjusted for the number of planned comparisons. Statistical analysis was performed using SPSS 13.

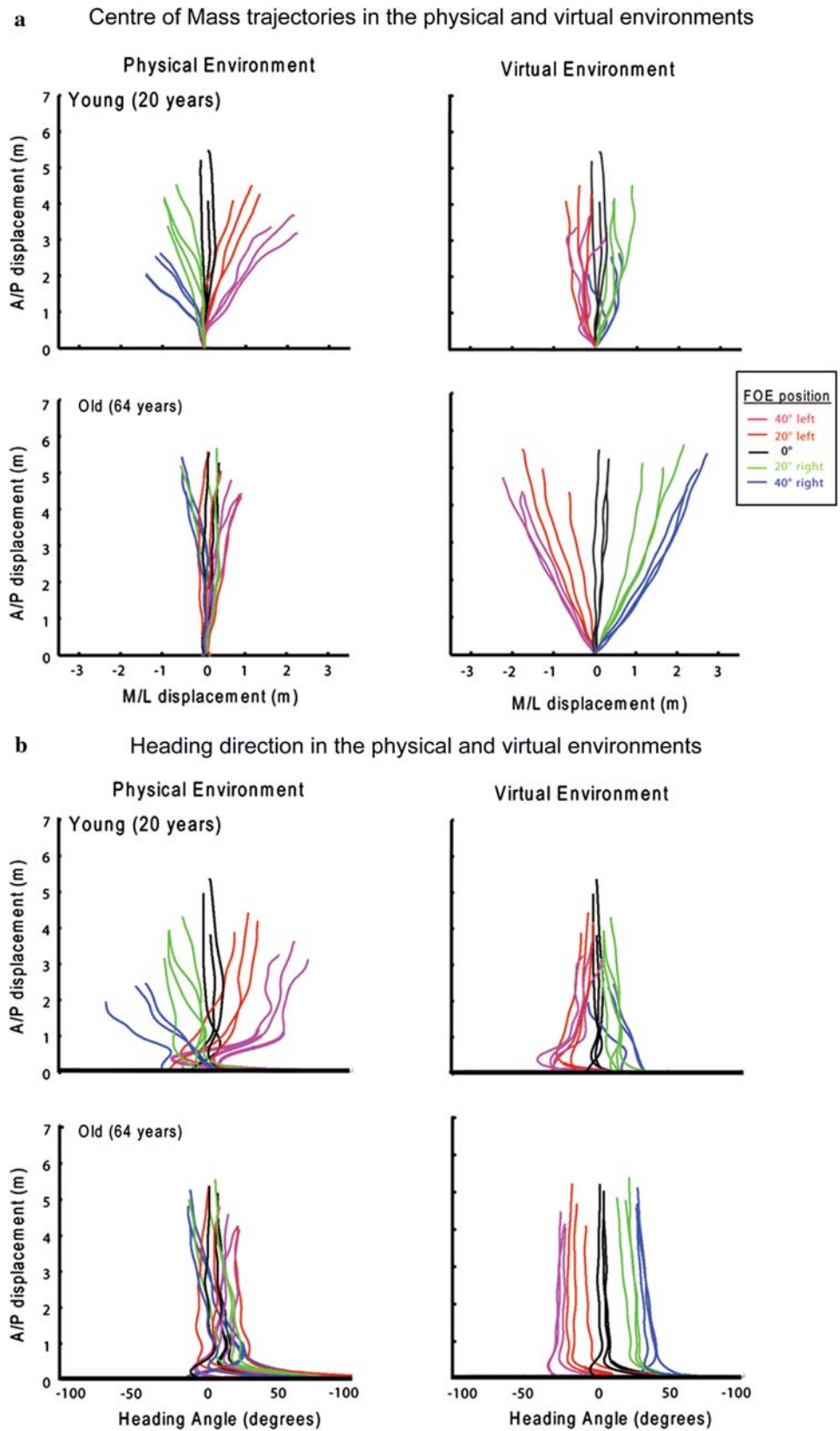
Results

CoM trajectory and heading error

As the task was to walk straight with respect to the virtual scene, a deviation of the CoM in the physical environment equal in magnitude and opposite to the displacement of the FOE (Fig. 1c) was expected if the task was perfectly accomplished. The same ‘perfect’ trajectory would yield a straight walking path and no heading error (0°) when plotted with respect to the virtual coordinates. Figure 2a shows representative data from one young and one older adult. Young adults adjusted their locomotor trajectory in response to the location of the optic flow by walking away from the FOE in the physical environment. However, they did not accomplish their instructed task perfectly as they still deviated their walking trajectory with respect to the VE. The older adults in this study were not strongly affected by optic flow cues, and typically maintained a nearly straight walking path in all conditions. The large deviation of their trajectories with respect to virtual coordinates reveals that they were not able to accomplish the task of walking straight in the VE. The heading direction calculated with respect to the virtual scene reflects the heading error of the subject. Figure 2b shows heading direction of one young and one older adult plotted with respect to both the physical and VEs. This example demonstrated how young participants made adjustments early in their trajectory and reduced their heading error as they progressed forward. Conversely, the older adults did not correct their heading errors and hence there was little change in their heading error over time.

Analysis of the CoM ML deviation (Fig. 3) revealed that there was an overall main effect due to age ($F_{(1,17)} = 6.57$, $P = 0.020$). There was also an interaction between age and FOE condition ($F_{(4,68)} = 8.623$, $P < 0.001$). Young adults deviated their CoM trajectories in the physical room away from the FOE (in each of the four conditions where FOE was shifted, $P < 0.001$). In contrast, older adults did not significantly alter their walking trajectories in the physical environment, regardless of the flow presented ($P > 0.05$). In terms of walking trajectories with respect to the VE, young adults still deviated from the virtual centre of the room when the FOE was displaced ($P < 0.001$; not illustrated) but there was a significant main effect due to age ($F_{(1,17)} = 7.353$, $P = 0.015$) on

Fig. 2 Representative data of CoM trajectory (**a**) and heading direction (**b**) in the horizontal plane (anteroposterior (AP) vs mediolateral (M/L) displacements) for one younger and one older adult. Each *line* represents a single trial and the location of the FOE is represented by the *colour* of the trajectory. The *graphs on the left and right columns* are the same data plotted with reference to the physical and virtual room coordinates, respectively



heading errors in the VE (Fig. 4). Older adults have greater virtual heading errors than young adults in all conditions where the FOE was offset ($P < 0.001$). Further,

there was also a significant main effect due to FOE location on the heading error ($F_{(1,68)} = 310.5$, $P < 0.001$). For both younger and older adults, heading error was

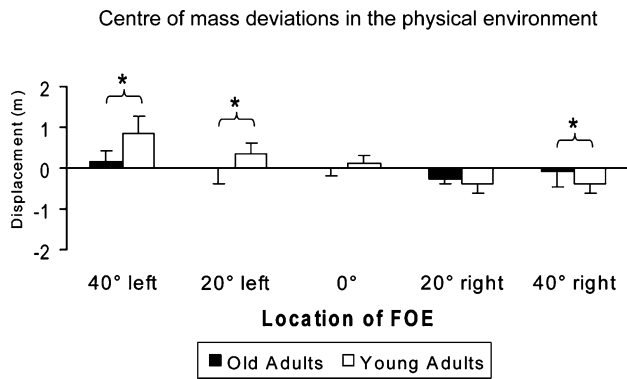


Fig. 3 Mean (± 1 SD) ML deviations of the CoM plotted with respect to the physical world in the younger vs older adults. Significant differences between groups are indicated ($*P < 0.01$)

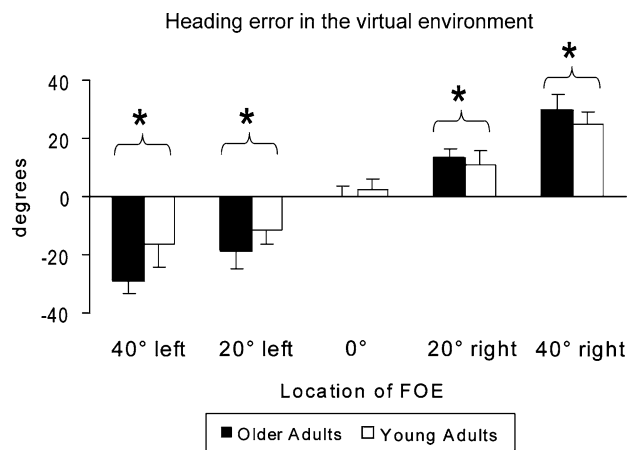


Fig. 4 Mean (± 1 SD) heading error in the virtual environment in the younger vs older adults. Heading error is defined as the angular orientation of the CoM trajectory in the virtual environment. If the goal to walk straight in the virtual environment is achieved, heading error would be equal to 0°. Positive values in degrees indicate rotation to the right. Significant differences between groups are indicated ($*P < 0.05$)

significantly larger than 0 in all conditions where the FOE was offset.

Segment orientation

Examination of segment orientations of the head, trunk and pelvis in the yaw direction revealed some interesting results. There were no effects due to FOE location on head orientation, however, significant interaction effects between groups and FOE position were present for the trunk ($F_{(1,68)} = 4.926, P = 0.002$) and pelvis ($F_{(1,68)} = 6.219, P < 0.001$). Young adults show no significant differences in head yaw across conditions ($P > 0.05$). In the presence of an FOE offset, however, there was significant trunk and pelvis yaw directed away from the FOE ($P < 0.001$). Together this suggests that the young adults adopted a strategy where

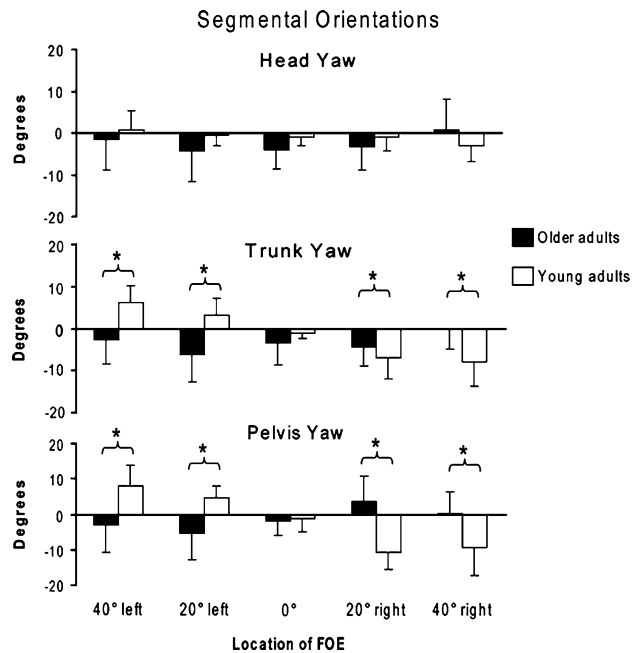


Fig. 5 Mean (± 1 SD) orientation of the head (a), trunk (b) and pelvis (c) for the two groups of subjects (young vs old). Positive values indicate rotation to the right. Significant differences between groups are indicated ($*P < 0.01$)

the head was orientated straight ahead, and the turn was achieved by rotating the body in the direction away from the FOE. In contrast, segmental control for the older adults remained unaffected by the direction of FOE presented (Fig. 5), with no significant differences due to FOE location for head, trunk or pelvis yaw ($P > 0.05$).

Discussion

The purpose of this study was to contrast the steering behaviours of young and older individuals in response to different directions of optic flow. In order to stay straight in the virtual scene, subjects had to physically walk in the direction opposite to the offset of the FOE. Our results indicate that young adults were able to adjust their locomotor heading in response to the flows presented by physically deviating their trajectory in the ML direction. The older adults, however, did not use the optic flow cues presented while walking despite being instructed to do so, and typically walked straight in the room, regardless of the direction of optic flow presented. This finding is intriguing in that it has been reported that older adults are more reliant on visual cues for postural tasks (Paquette et al. 2006) and locomotion (Chapman and Hollands 2006), yet our results indicate that this effect may be context-dependent.

The young adults in our study were able to use the optic flows presented, but they were still not able to perfectly

accomplish the task demands. While the heading errors were smaller than those of the older adults, they were not perfectly neutral, indicating that the central nervous system (CNS) does not rely solely on vision and down-regulate other sensory cues in the control of heading for this particular task. Examination of the segmental orientations of the young subjects revealed that CoM deviations were achieved by using a side-stepping strategy, without any rotations of the head, similar to what has been reported by others using a translational flow to offset the FOE (Warren Jr et al. 2001; Sarre et al. 2008). The young adults in this study did not adopt the characteristic strategy of first reorienting the eyes, then the head, and trunk, which is typically seen while turning (Grasso et al. 1996; Hollands et al. 2001). Instead, our young subjects kept the head aligned in the physical, straight-ahead position and allowed for some small rotations of the lower segments. This side-stepping strategy has been described previously and is likely related to the type of flow presented (Sarre et al. 2008).

In contrast, the older adults showed no locomotor deviation in response to the different flows presented. Our older subject population was in fact not very old (60–72 years). It is striking that there are already such large aging effects despite that this group is what is often described as ‘young-old’. These effects might have been even more pronounced if older subjects were used. The reason for the lack of adjustments in older adults is unclear.

Differences between the older and young groups may be related to the slower walking speed of the older adults. The rate of optic flow offset was a function of the forward displacement. The average gait speed of the older adults was significantly ($P < 0.01$) slower than that of the young subjects (0.75 ± 0.23 and 0.92 ± 0.20 m/s, respectively), which means that the older group did receive slower flow than their younger counterparts. The flow rates for the young and older subjects in the 20° condition was $1.7^\circ/\text{s}$ and $1.4^\circ/\text{s}$, respectively, and $3.8^\circ/\text{s}$ and $3.1^\circ/\text{s}$, respectively, for the 40° condition. Others have argued that at similar flow rates, 2–5°/s extra-retinal cues are required to make accurate heading judgements (Royden et al. 1994; Banks et al. 1996) but, at slower rotation rates, accurate heading discriminations can be made from retinal flow characteristics alone (Warren Jr and Hannon 1988, 1990). If anything, the slightly slower rates of the older adults would be easier to interpret given that extra-retinal cues (which may not be used to decompose slower flow rates) are actually in conflict of what is being presented on the screen. Given this, it is doubtful that the difference between the age groups is due to the slower gait speed in the older group.

It is possible that older adults have altered perception of visual motion, which makes it difficult for the CNS to integrate the visual information into the locomotor command. Snowden and Kavanagh (2006) have reported that older

adults have higher minimum motion thresholds than younger adults across all spatial frequencies. Moreover, older adults have higher motion coherence thresholds than younger adults (Trick and Silverman 1991; Snowden and Kavanagh 2006), which may also cause them to perceive less motion in the virtual scene and thus would make smaller corrections in the physical environment. However, in this study, it is unlikely that the differences between the older and younger subjects can be completely attributed to altered visual motion perception due to aging. We presented subjects with strong optic flow cues, in a richly textured scene and the FOE offsets were considerably large (20° and 40°). As a result, the visual cues given in this work likely exceeded the lower level differences associated with aging that have been reported for minimum motion threshold and motion coherence levels. Furthermore, it is important to consider the type of visual motion that subjects in this study experienced. In this experiment, the offsetting of the FOE while moving through the VE produced a radial flow pattern (as opposed to simple lamellar flow).

Recently, it has been reported that older adults showed no impairments in the perception of radial flows (Billino et al. 2008). Such findings are in contrast to the higher thresholds for discrimination of heading direction from a radial flow pattern reported by Warren Jr et al. (1989). The reason for the discrepancy is unclear, however, Billino et al. (2008) used much higher displacement of the FOE (5.6°) than the reported minimum threshold reported by Warren et al. (1.9°). If older adults retain the ability to discriminate radial flow patterns at higher FOE shifts, then, given the magnitude of the FOE shifts experienced by our participants, our results indicating differences between older and younger participants cannot be attributed to an inability to perceive the changing optic flows.

Rather than having deficits perceiving optic flows, older adults may have difficulty making on-line adjustments to changing optic flows. It is plausible that the older adults in our study had difficulty re-weighting sensory inputs for the control of locomotor steering. In this study design, the visual information is in conflict with other sources of sensory feedback. Proprioceptive feedback from the eyes and head, efferent signals to the extra-ocular and neck muscles, and vestibular signals have been implicated in the control of heading (e.g. Royden et al. 1992, 1994; Banks et al. 1996; Crowell et al. 1998; Vallis and Patla 2004) and are in conflict with the virtual scene presented to our subjects. The task that we asked the subjects to perform (‘walk straight in the virtual scene’) requires participants to recalibrate the visuomotor systems and basically ignore other in-coming sensory information and rely solely on visual cues. It has been reported that older adults have greater postural instability not only when visual cues are removed, but also when they are re-inserted,

or are incongruent (Teasdale et al. 1991; Simoneau et al. 1999; Bugnariu and Fung 2007; O'Connor et al. 2008), suggesting that aging affects the ability to appropriately re-weight the available sensory information in an on-line manner for postural tasks. Our data suggest that sensory re-weighting may also be affected by aging during locomotor tasks. Indeed in other locomotor tasks it has been demonstrated that older adults can adjust their locomotor behaviour in response to changing optic flow speeds (Lamontagne et al. 2007). A previous study presented older adults with changing optic flow speeds while walking on a self-paced treadmill (Lamontagne et al. 2007) showed that they were able to modulate their walking velocity to match the optic flow presented. Since there were no healthy young subjects tested in that previous study, it remains unclear how speed modulation is affected by aging. The ability of older adults to use optic flow appears to be dependent on the task being performed, and possibly on the type of flow presented. The optic flow presented to our subjects was offset by using a translation of FOE in the ML direction. Recently it has been shown that different types of optic flows elicit different locomotor responses (Sarre et al. 2008). It would be interesting to investigate how older adults adapt to other types of optic flow, such as rotational flows that may be more ecologically relevant.

This study reveals that older adults were unable to use optic flow cues to guide their locomotor heading, even when specifically instructed. The fact that older adults often have difficulty coping with steering and turning tasks may reflect an inherent inability to recalibrate the visuomotor system in a timely manner. Such difficulty may also explain why there is a high incidence of falls reported during activities where a lot of dynamic visual information is present, such as that involved during walking and turning. Further work investigating the underlying sensorimotor integration mechanisms is warranted.

Acknowledgements The authors would like to thank all the participants of the study, as well as Christian Beaudoin and Maxim Hanna for their technical assistance. This study was funded by an operating grant from the Canadian Institute of Health Research (CIHR). J. Berard is the recipient of a training award funded jointly by the CIHR and the Heart and Stroke Foundation of Canada.

References

- Banks MS, Ehrlich SM, Backus BT, Crowell JA (1996) Estimating heading during real and simulated eye movements. *Vision Res* 36:431–443
- Billino J, Bremmer F, Gegenfurtner KR (2008) Differential aging of motion processing mechanisms: evidence against general perceptual decline. *Vision Res* 48:1254–1261
- Bugnariu N, Fung J (2007) Aging and selective sensorimotor strategies in the regulation of upright balance. *J Neuroeng Rehabil* 4:19
- Chapman GJ, Hollands MA (2006) Age-related differences in stepping performance during step cycle-related removal of vision. *Exp Brain Res* 174:613–621
- Crowell JA, Banks MS, Shenoy KV, Andersen RA (1998) Visual self-motion perception during head turns. *Nat Neurosci* 1:732–737
- Gibson JJ (1966) *The perception of the visual world*. Houghton Mifflin, Boston
- Grasso R, Glasauer S, Takei Y, Berthoz A (1996) The predictive brain: anticipatory control of head direction for the steering of locomotion. *Neuroreport* 7:1170–1174
- Hollands MA, Sorensen KL, Patla AE (2001) Effects of head immobilization on the coordination and control of head and body reorientation and translation during steering. *Exp Brain Res* 140:223–233
- Huitema RB, Brouwer WH, Mulder T, Dekker R, Hof AL, Postema K (2005) Effect of ageing on the ability to adapt to a visual distortion during walking. *Gait Posture* 21:440
- Lamontagne A, Fung J, McFadyen B, Faubert J (2007) Modulation of walking speed by changing optic flow in persons with stroke. *J Neuroeng Rehabil* 4:22
- Lipsitz LA, Jonsson PV, Kelley MM, Koestner JS (1991) Causes and correlates of recurrent falls in ambulatory frail elderly. *J Gerontol* 46:M114–M122
- Lord SR (2006) Visual risk factors for falls in older people. *Age Ageing* 35:ii42–ii45
- Lord SR, Webster IW (1990) Visual field dependence in elderly fallers and non-fallers. *Int J Aging Hum Dev* 31:267–277
- Nevitt MC, Cummings SR (1994) Type of fall and risk of hip and wrist fractures: the study of osteoporotic fractures. *J Am Geriatr Soc* 42:909
- Norman JF, Dawson TE, Butler AK (2000) The effects of age upon the perception of depth and 3-D shape from differential motion and binocular disparity. *Perception* 29:1335–1359
- O'Connor KW, Loughlin PJ, Redfern MS, Sparto PJ (2008) Postural adaptations to repeated optic flow stimulation in older adults. *Gait Posture* 28:385–391
- Paquette C, Paquet N, Fung J (2006) Aging affects coordination of rapid head motions with trunk and pelvis movements during standing and walking. *Gait Posture* 24:62–69
- Paquette MR, Fuller JR, Adkin AL, Vallis LA (2008) Age-related modifications in steering behaviour: effects of base-of-support constraints at the turn point. *Exp Brain Res* 190:1–9
- Royden CS, Banks MS, Crowell JA (1992) The perception of heading during eye movements. *Nature* 360:583
- Royden CS, Crowell JA, Banks MS (1994) Estimating heading during eye movements. *Vision Res* 34:3197
- Sarre G, Berard J, Fung J, Lamontagne A (2008) Steering behaviour can be modulated by different optic flows during walking. *Neurosci Lett* 436:96–101
- Schiff W, Oldak R, Shah V (1992) Aging persons' estimates of vehicular motion. *Psychol Aging* 7:518–525
- Scialfa CT, Guzy LT, Leibowitz HW, Garvey PM, Tyrrell RA (1991) Age differences in estimating vehicle velocity. *Psychol Aging* 6:60–66
- 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
- Snowden RJ, Kavanagh E (2006) Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds. *Perception* 35:9–24
- Teasdale N, Stelmach GE, Breunig A (1991) Postural sway characteristics of the elderly under normal and altered visual and support surface conditions. *J Gerontol* 46:B238–B244
- Trick GL, Silverman SE (1991) Visual sensitivity to motion: age-related changes and deficits in senile dementia of the Alzheimer type. *Neurology* 41:1437–1440

- Vallis LA, Patla AE (2004) Expected and unexpected head yaw movements result in different modifications of gait and whole body coordination strategies. *Exp Brain Res* 157:94–110
- Warren WH Jr, Hannon DJ (1988) Direction of self-motion is perceived from optical flow. *Nature* 336:162
- Warren WH Jr, Hannon DJ (1990) Eye movements and optical flow. *J Opt Soc Am A* 7:160–169
- Warren WH Jr, Blackwell AW, Morris MW (1989) Age differences in perceiving the direction of self-motion from optical flow. *J Gerontol* 44:147–153
- Warren WH Jr, Kay BA, Zosh WD, Duchon AP, Sahuc S (2001) Optic flow is used to control human walking. *Nat Neurosci* 4:213–216