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Stroke Affects Locomotor Steering Responses to Changing Optic Flow Directions

Anouk Lamontagne, PhD,1 Joyce Fung, PhD,1 Bradford McFadyen, PhD,2 Jocelyn Faubert, PhD,3 and Caroline Paquette, PhD1

Abstract
Background. Stroke patients manifest steering difficulties during walking, which may arise from an altered perception of visual motion. Objective. To examine the ability of stroke patients to control their heading direction while walking in a virtual environment (VE) describing translational optic flows (OFs) expanding from different directions. Methods. The authors evaluated 10 stroke patients and 11 healthy people while they were walking overground and visualizing a VE in a helmet-mounted display. Participants were instructed to walk straight in the VE and were randomly exposed to an OF having a focus of expansion (FOE) located in 5 possible locations (0°, ±20°, and ±40° to the right or left). The body’s center of mass (CoM) trajectory, heading direction, and horizontal body reorientation were recorded with a Vicon-512 system. Results. Healthy participants veered opposite to the FOE location in the physical world, with larger deviations occurring at the most eccentric FOE locations. Stroke patients displayed altered steering behaviors characterized either by an absence of CoM trajectory corrections, multiple errors in the heading direction, or systematic veering to the nonparetic side. Both groups displayed relatively small CoM trajectory corrections that led to large virtual heading errors. Conclusions. The control of heading of locomotion in response to different OF directions is affected by stroke. An altered perception of heading direction and/or a poor integration of sensory and motor information are likely causes. This altered response to OF direction while walking may contribute to steering difficulties after stroke.

Keywords
heading, hemiparesis, kinematics, virtual reality, visual motion, walking

Introduction
The control of steering, or heading direction, is a requirement for goal-directed locomotion, allowing individuals to walk in the desired direction while avoiding obstacles along their path. Such control depends heavily on vision that provides information about the characteristics of the surrounding world and self-motion. Optic flow (OF) is a predictable pattern of visual motion generated at the moving eye during self-motion.1 Together with the perceived goal direction, it is one of the visual cues that can be used to control heading direction while walking.2-4 When walking straight, the OF describes a radial pattern of expansion with a focus of expansion (FOE) located in the direction of heading.4 When a change of direction is needed, the OF theory stipulates that the FOE is realigned with the desired heading direction.1 In support of this theory, it has been shown that offsetting the FOE of OF with prisms or through virtual reality causes healthy individuals to veer from their initial trajectory when instructed to walk straight ahead.2-4 Individuals who sustained a stroke are especially challenged in their daily activities as they have difficulties adapting their locomotion to environmental constraints. They show disrupted eye and body movement coordination patterns and altered walking trajectories when executing preplanned or cued changes of direction while walking, suggesting disrupted steering abilities.5,6 The loss of balance from executing a sudden turn of the head or body can result in a fall.7 Although motor deficits undoubtedly impair

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steering abilities, sensory deficits and altered sensorimotor integration are also likely to be involved. The ability to process different types of visual motion was shown to be altered by brain lesions in the occipitoparietal, parietotemporal, and posterior parietal regions possibly involving the MT (V5) complex. It would also be affected by a lesion of the frontal lobe. Whether such altered perception of OF direction translates into poor steering abilities after stroke, however, is not known.

The goal of this study was to examine the ability of individuals with stroke to control their heading direction while walking in a virtual environment (VE) describing translational OFs expanding from different directions. It was hypothesized that these individuals would display an altered control of their heading direction in response to the shifts in the foci of expansion, as reflected either by reduced adjustments and/or directional errors in their walking trajectories.

Methods
Participants

A convenience sample of 10 patients with stroke and 11 healthy persons participated in the study (Table 1). The 2 groups were of the same age (t test, P = .12) and presented similar anthropometric characteristics. The inclusion criteria for the patients were the following: a first unilateral stroke in the middle cerebral artery (MCA) territory with residual deficits, confirmed by computerized tomography; walking independently over 10 m, with or without a walking aid, at a walking speed inferior to 1.0 m/s; and presenting with significant motor deficits of the affected lower limb, as reflected by a Chedoke-McMaster leg and foot impairment inventory score of less than 7. Exclusion criteria for the patients were the following: cognitive problems compromising the ability to give informed consent and to follow instructions as well as the presence of a visual field defect, as assessed by the Goldman visual field and/or equivalent computerized test. Patients with stroke were also free of visual spatial neglect, as assessed by the Bell’s Test or Star Cancellation Test, except for 2 of them (Table 1, patients S3 and S4) who were enrolled in the study before neglect was confirmed. When appropriate, the behavior of these 2 patients is described separately. Both healthy participants and those with stroke were free of visual problems not corrected by eyewear as well as of other neurological or orthopedic conditions interfering with locomotion. All participants signed an informed consent document, and the project was approved by the Montréal Center for Interdisciplinary Research in Rehabilitation (CRIR) establishments’ Research Ethics Board.

Setup and Procedures

Participants were evaluated while walking overground at their comfortable speed in a large open space (12 m × 8 m), with their walking aid when applicable (see walking aid description, Table 1). They were visualizing, in a helmet-mounted display (HMD) unit, a VE representing a large (40 m × 25 m) and symmetrical room created in Softimage XSI (Figure 1A). The virtual room was created to provide a rich-textured VE and had pillars at its extremities, which were separated by 8 m. The HMD (Kaiser Optics ProView XL50) had a field of view of 50° diagonal, 30° vertical by 40° horizontal. Three-dimensional body coordinates were recorded using a 10-camera Vicon-512 motion capture system (Denver, CO). Passive reflective markers were located on specific body landmarks according to the Plug-In-Gait Model from Vicon, except for the head that was represented by a 3-marker model with markers located on the front, left side, and right side of the HMD. Location of the body’s center of mass (CoM) was calculated based on a 15-segment kinematic model and the anthropometric characteristics of the participants. The 3D head coordinates were tracked in real time by the Tarsus real-time engine from Vicon and fed to the Caren-2 virtual reality system from Motek (Motek Medical, Amsterdam). This feedback system synchronized the virtual scene in real time with head motions through the physical space (Figure 1B). When applicable, a visual perturbation could also be superimposed onto the motion of the scene caused by the head displacements of the participants. The delay in updating the virtual reality display in the HMD is less than 10 ms. The sampling frequency was set at 120 Hz.

As they were walking forward, participants were exposed to a translational OF that was expanding from a FOE located in 5 possible locations (Figure 1C): −40° and −20° to the left or nonparetic side, 0°, as well as +20° and +40° to the right or paretic side. A FOE angular offset (θ) was obtained by translating the scene laterally (x) based on the participant’s forward displacement (y), such that x = ytan(θ). Based on the forward walking speed of the participants, this corresponds to average rates of mediolateral translation of the scene of 0.32 m/s (±40° FOE) and 0.14 m/s (±20° FOE) for the patients and to 0.64 m/s (±40° FOE) and 0.28 m/s (±20° FOE) for the healthy controls. Participants were instructed to walk straight in the VE, that is, “walk straight with respect to the scene they were visualizing in the HMD,” as opposed to the physical world. For a FOE located at 20° to the right, for instance, participants should perceive their virtual heading direction as translating forward and toward the right (Figure 1D). In an attempt to walk straight, they should veer to the left in the physical world, such that their walking trajectory remains around neutral (0°) in the virtual world. They
Table 1. Participant Characteristics

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Age (years)</th>
<th>Gender</th>
<th>Height (cm)</th>
<th>Weight (kg)</th>
<th>Speed (m/s)</th>
<th>Time Since Stroke</th>
<th>Neglect (Y/N)</th>
<th>Side of Lesion</th>
<th>Etiology</th>
<th>Location of Cerebrovascular Accident</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>50</td>
<td>M</td>
<td>173</td>
<td>75</td>
<td>0.80</td>
<td>3.4 Months</td>
<td>N</td>
<td>L</td>
<td>Ischemia + small hemorrhage</td>
<td>Temporoparietal junction, insular cortex</td>
<td></td>
</tr>
<tr>
<td>S2</td>
<td>79</td>
<td>M</td>
<td>176</td>
<td>73</td>
<td>0.35 (Cane)</td>
<td>2.7 Months</td>
<td>N</td>
<td>R</td>
<td>Ischemia, lacunar</td>
<td>Subcortical, postinternal capsule</td>
<td></td>
</tr>
<tr>
<td>S3</td>
<td>71</td>
<td>M</td>
<td>178</td>
<td>72</td>
<td>0.15 (Quad)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.4 Months</td>
<td>Y</td>
<td>L</td>
<td>Massive Ischemia</td>
<td>Frontotemporoparietal, basal ganglia</td>
<td></td>
</tr>
<tr>
<td>S4</td>
<td>66</td>
<td>M</td>
<td>152</td>
<td>68</td>
<td>0.18 (Quad)</td>
<td>1.9 Months</td>
<td>Y</td>
<td>R</td>
<td>Ischemia + small hemorrhage</td>
<td>Frontotemporoparietal, basal ganglia; caudate and thalamus spared</td>
<td></td>
</tr>
<tr>
<td>S5</td>
<td>73</td>
<td>F</td>
<td>155</td>
<td>48</td>
<td>0.3 (Cane)</td>
<td>2.9 Months</td>
<td>N</td>
<td>L</td>
<td>Ischemia</td>
<td>Parietal, external capsule, and lenticular nucleus</td>
<td></td>
</tr>
<tr>
<td>S6</td>
<td>79</td>
<td>M</td>
<td>152</td>
<td>60</td>
<td>0.60 (2 Canes)</td>
<td>2.1 Months</td>
<td>N</td>
<td>L</td>
<td>Ischemia</td>
<td>Parietal</td>
<td></td>
</tr>
<tr>
<td>S7</td>
<td>51</td>
<td>M</td>
<td>185</td>
<td>96</td>
<td>0.66</td>
<td>5.0 Months</td>
<td>N</td>
<td>R</td>
<td>Ischemia</td>
<td>Subcortical, capsulothalamic</td>
<td></td>
</tr>
<tr>
<td>S8</td>
<td>73</td>
<td>F</td>
<td>154</td>
<td>90</td>
<td>0.34</td>
<td>1.0 Months</td>
<td>N</td>
<td>L</td>
<td>Ischemia</td>
<td>Parietal periventricular region, thalamus</td>
<td></td>
</tr>
<tr>
<td>S9</td>
<td>68</td>
<td>M</td>
<td>162</td>
<td>50</td>
<td>0.20 (Cane)</td>
<td>2.2 Months</td>
<td>N</td>
<td>R</td>
<td>Intraparenchymal hemorrhage</td>
<td>Parietal</td>
<td></td>
</tr>
<tr>
<td>S10</td>
<td>79</td>
<td>M</td>
<td>172</td>
<td>70</td>
<td>0.20 (Quad)</td>
<td>3.0 Months</td>
<td>N</td>
<td>R</td>
<td>Ischemia</td>
<td>Capsulothalamic&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>69</td>
<td>—</td>
<td>166</td>
<td>70</td>
<td>0.44</td>
<td>1.26</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>11</td>
<td>—</td>
<td>12</td>
<td>15</td>
<td>0.23</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>Controls (n = 11)</td>
<td></td>
<td></td>
<td>152-185</td>
<td>48-96</td>
<td>0.20-0.80</td>
<td>1-51 Months</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
</tr>
</tbody>
</table>

Abbreviation: SD, standard deviation.

<sup>a</sup>Individuals with stroke were assigned to different groups depending on their steering behaviors, as described in the Results section. (1) Minimal Veering Group; (2) Incongruous Veering Group; and (3) Nonparetic Veering Group.

<sup>b</sup>The quad cane is a 4-legged cane.

<sup>c</sup>Initial scans were negative. A subsequent report states the presence of a subcortical infarct in this patient having a contralateral sensorimotor involvement of the hemibody with mild dysarthria and dysphagia.
were provided with 3 to 5 practice trials, with and without perturbations, before the experiments. We also confirmed verbally that they understood the instruction, both prior to and after the data collection. Three trials per FOE location were recorded, for a total of 15 walking trials. Because of their limited endurance, participants with stroke succeeded in performing 2 to 3 trials per FOE location. An assistant was standing next to or walking along with the

Figure 1. This figure shows (A) the virtual room used for the experiment, (B) the control algorithm of the virtual environment (VE) is based on real-time tracking of head coordinates, (C) the different locations of the focus of expansion (FOE) used in the present experiment, and (D) a schematic representation of perceived, physical, and virtual walking trajectories.
participants at all times, and no falls occurred during the experiment.

Outcome variables retained for analysis included CoM trajectory and horizontal orientations of head and feet with respect to the physical and virtual world’s coordinates. Displacement and angular orientation toward the right (controls) or the paretic side (stroke) are referred to as positive. In addition, heading direction was computed as the instantaneous angular orientation of body CoM trajectory along the mediolateral (x-axis) versus the anteroposterior (y-axis) direction. For every trial, heading orientation in the virtual world, also termed as virtual heading error, was estimated as the mean heading orientation measured between 2 m and 3 m of forward walking. When 3 m of forward walking could not be reached, the mean value between 2 m and maximal forward walking distance was used instead. Mean virtual heading errors were thereafter averaged across trials and participants. By convention, a negative heading error refers to an underestimation of the correction needed to reach a virtual heading of 0°, whereas a positive heading error means that participants overcorrected their walking trajectory. Within- and between-participant variabilities were obtained using standard deviation values calculated across trials and participants, respectively. Virtual heading errors and within-participant variability were compared across groups (stroke vs controls) and conditions (FOE location, 5 levels) using a 2-way analysis of variance for repeated measures. The relationships of the virtual heading errors with gait speed and age were assessed using Pearson correlation coefficients. Statistics were performed in Statistica with a level of significance accepted at \( P < .05 \).

Results

Examples of CoM trajectory modulation of healthy participants in response to different FOE locations are illustrated in Figure 2. To help understand what a typical profile of modulation looks like, an example of a healthy elderly control is contrasted with that of a healthy young individual. For both participants, the CoM trajectory and heading
orientation in the physical world were characterized by a deviation in the direction opposite to the FOE location (left and middle panels). The amplitudes of the CoM trajectory and the heading corrections were scaled to the magnitude of the perturbation, being larger for the 40° than for the 20° and 0° perturbations. The healthy young individual displayed large yet incomplete heading corrections in the physical world (middle panel), resulting in heading errors that were biased toward the FOE location in the virtual world (right panel). This participant’s heading error, however, decreased in the virtual world and converged toward the midline (0°) as he continued walking forward. In comparison, the healthy elderly control presented with much smaller heading corrections in the physical world, resulting in larger heading errors in the virtual world.

In comparison with healthy controls, stroke patients presented with a variety of steering behaviors, including heading corrections that were of the wrong magnitude and/or in the wrong direction (Figure 3). Based on the steering behavior, patients were classified into 3 different groups. The Minimal Veering Group (n = 3) presented with little or no modulation of their CoM trajectory and heading orientation in the physical world when exposed to FOE shifts. As a result, they displayed large heading errors in the virtual world that were approaching the magnitude of the FOE shifts. The Incongruous Veering Group (n = 3) displayed...
multiple and inconsistent directional errors, with heading corrections being made erratically sometimes toward the paretic and sometimes toward the nonparetic side for similar FOE perturbations. The Nonparetic Veering Group (n = 3) veered to their nonparetic side in the physical world for most trials, regardless of the FOE location. This means that when the FOE was on the paretic side, participants corrected their heading in the expected direction by veering to their nonparetic side. When the FOE was shifted to the nonparetic side, however, they veered in the wrong direction, that is, the ipsilateral nonparetic side. This resulted in larger virtual heading errors for the paretic than the nonparetic side. Note that the 2 participants with stroke who had visuospatial neglect (S3 and S4) were included in the Minimal Veering Group and the Nonparetic Veering Group, respectively. One remaining participant with stroke (S2), not included in the 3 groups, displayed behavior identical to that of the healthy controls.

An example of CoM trajectory modulation as well as of head and foot orientation is further detailed in Figure 4 for a healthy control and a stroke patient with visuospatial neglect. The CoM trajectory of the healthy control veered in the direction opposite to the FOE location in the physical world, but the correction remained incomplete, leading to some deviation error in the virtual world. The feet were aligned with the CoM trajectory in the physical world, but the head showed few changes in its orientation with FOEs of changing location. This head and foot orientation pattern is typical of what was observed in the healthy control group as well as in most participants with stroke. Alternatively, the patient with visuospatial neglect represented in Figure 4 invariably veered to the nonparetic side, irrespective of the FOE location. As for the other patients in group 2, a directional error arose when the FOE was located toward the nonparetic side, which did not cause the patient to veer toward the paretic side in the physical world, as would be expected normally. For the patient shown in Figure 4, his head and nonparetic foot were oriented toward the nonparetic side in the physical world, whereas the paretic foot remained in a more toes-out and widened position.

Figure 4. Individual trials representing CoM trajectory as well as head and foot horizontal orientation in the physical and virtual worlds for 1 healthy control and 1 patient (S4) with visuospatial neglect.
The average heading orientations in the virtual world, or heading errors, were compared between patients and healthy participants across FOE locations (Figure 5). All participants undercorrected their heading in response to FOEs of changing direction. Virtual heading errors increased at more eccentric FOE locations, both for patients and healthy participants ($P < .01$). Given the different behaviors observed in the stroke patients, their mean virtual heading errors...
were found to be similar to those of the healthy participants \( (P > .05) \), despite a tendency for larger heading errors in the patients at \( \pm 40^\circ \) of FOE perturbation. Within-participant and between-participant variabilities in the heading responses, however, were larger in the patients than in the healthy group \( (P < .05; \text{within-participant}) \). Heading errors of patients and healthy participants were not correlated with walking speed \( (R^2 = 0.00-0.07; P > .05) \) or age \( (R^2 = 0.00-0.19; P > .05) \). A qualitative analysis of the heading behavior of patients with respect to the lesion site or the use of walking aids did not reveal any identifiable relationships (Table 1).

**Discussion**

This study provides the first evidence that individuals who sustained a stroke can manifest altered locomotor steering behaviors when exposed to OFs expanding from different locations. Such altered behaviors are reflected by abnormally small adaptations and/or by directional errors in the participants’ walking trajectories as well as by an increased variability across trials. The present results are consistent with the attenuated and/or altered gait speed modulation responses of participants with stroke when exposed to OFs of changing speeds.\(^{16}\)

It has been shown that healthy young individuals exposed to an artificially shifted FOE while walking veer in the direction opposite to the goal in the physical world so that a virtual heading error close to zero can be reached.\(^{4}\) We have also shown that the larger the shift in the FOE, the larger the walking trajectory deviation in the physical world, and the larger the virtual heading error.\(^{3}\) In other words, the corrections in the physical walking trajectory are insufficient to lead to straight walking trajectories in the virtual world, and the heading errors increase at more eccentric locations of FOE. Present data collected in healthy controls who are older than the young individuals tested previously in other studies do support these observations.

**Brain Lesion and Altered Heading Perception**

An absence of response characterized the Miminal Veering Group, and multiple heading errors were displayed by the Incongruous Veering Group. No qualitative relationship could be established between the patterns of heading responses and the localization of the brain lesion. It cannot be excluded that the different heading behaviors (absence of responses vs errors) may just be different expressions of the same inability to perceive or use OFs to complete the heading task. It is worth investigating, however, whether the damaged brain areas of our participants could lead to an altered discrimination of visual motion direction and heading. The intact human brain shows activation in the occipital, parietal, and temporal cortical areas while viewing radial OFs.\(^{17}\) The human MT (V5) complex, and more specifically the MST area, were shown to be highly sensitive to changes in the characteristics of the OF stimuli.\(^{17,18}\)

Discriminating heading, depending on the nature of the visual stimulus, would involve a complex network comprising posterior brain areas such as KO and V3a,\(^{19-21}\) the MT complex,\(^{20,22}\) temporoparietal and occipitotemporal areas,\(^{19,20}\) and even frontal areas\(^{12,22}\) and subcortical/limbic structures.\(^{19}\) Altered processing of visual motion direction has been previously reported in participants with a stroke in the occipitoparietal, parietotemporal, or posterior parietal brain areas, which were all believed to involve the MT complex.\(^{8-11}\) In the present study, the MCA territory lesions would spare the posterior visual areas supplied by the posterior cerebral artery, but the MT complex, potentially supplied by both the MCA and posterior cerebral artery, could not be excluded. Some of our patients also presented hemorrhagic events, which potentially extended the lesion beyond the MCA territory. It is noteworthy that our patients who displayed altered steering behaviors had lesions that invariably involved the parietal lobe and/or thalamus. The parietal area is a key site for the integration of multiple sources of sensory information,\(^{23,24}\) and it is involved in the control of steering.\(^{25}\) The thalamus relays sensory information to different cortical areas, contributing crucially to motor actions. It seems reasonable to assume that lesions in such areas affect multisensory integration and can alter heading behaviors. Some of our patients also displayed lesion involving the frontotemporal region. There is evidence from intact or damaged brain studies that the frontal lobe,\(^{12}\) and more specifically the dorsal premotor area,\(^{22,25}\) is involved in heading identification. Those studies involved a ground plane or a radial OF pattern, which can resemble the type of stimulus used in the present study. According to Peuskens et al.,\(^{22}\) such activation in the dorsal premotor area could be “...a final stage in a parieto-premotor visuomotor connection, specifically related to transformation of heading information...into motor schemes.”\(^{\text{NP 2460}}\) In light of those findings, it appears likely that our patients had brain lesions that altered the perception and/or integration of heading information.

**Altered Sensorimotor Integration and Visuomotor Control**

The present paradigm also involved a sensory scenario in which visual stimuli were incongruent with proprioceptive and vestibular information. The central nervous system has the ability to reweight relevant sources of sensory information in a context-dependent fashion to maintain postural equilibrium.\(^{26-28}\) The transient aftereffect of self-motion experienced after treadmill running\(^{29}\) is another indirect
Visuospatial Neglect

Perhaps one of the most unexpected findings of the present study was the behavior observed in the Nonparetic Veering Group, which consisted of walking trajectories consistently deviating to the nonparetic side in the physical world. Closer examination of present data reveals that the directional error occurred when the FOE was located on the nonparetic side, which should have caused a turn to the paretic side. This is not likely to be a result of biomechanical factors because those with stroke tend to walk with a horizontal rotational bias of their body toward their paretic side, therefore, favoring a physical turn toward the paretic side. It has also been demonstrated that looking to the side at an object causes a slight curvature in one’s walking trajectory toward the direction of gaze. In the absence of reliable vision cues such as when walking blindfolded, a walking trajectory deviation contralateral to the eye or head rotation is observed instead.

In the present study, head and foot starting positions were aligned with the room’s coordinates before the participants started to walk, but the eyes might have been oriented in one or another direction. Even if this was the case, however, the effect would be very limited as in Jahn et al., for instance, a gaze rotation of 35° leads to a small trajectory deviation of 2° to 4°. Results of our study also show that one of the participants of the Nonparetic Veering Group had neglect, whereas the 2 others were theoretically free of such problems. In neglect, the paretic hemispace is less attended, and the subjective midline would be displaced to the nonparetic or ipsilesional side. This predicts that those with neglect should steer toward their paretic side in an attempt to walk straight, a prediction that is not supported by the present results. In reality, there is conflicting evidence as to whether those with neglect veer to their paretic or nonparetic sides as they walk. It also remains possible that some of our participants might have had far extrapersonal space neglect that was not picked up by paper-pencil tests.

Limitations

Our results outline the within-individual and interindividual variability of behavior usually observed in stroke. Given the exploratory nature of this study, inclusion criteria were purposely kept large, but factors such as walking capacity, chronicity, and the extent of the brain lesion may have contributed to the heterogeneity of behaviors. The nature of the brain imaging tool (CT scans) and variability in the depth of the information available in the patients’ charts also limited our interpretation of results in terms of the lesion site and its effects on heading behaviors. It is hoped that higher resolution imaging tools will help shed light on the role of specific brain areas in locomotor steering behaviors. Factors such as attention and the sense of presence (sense of “being there,” within the VE), which have not been quantified in this study, may also differ between those with stroke and healthy participants and account for some of the differences between the 2 groups. It could also be argued that gait speed, which was slower in the stroke participants, was partly responsible for their altered behavior. Indeed, walking faster or running, as compared with walking slower, reduces the deviations in walking trajectory when walking with shifted OFs, blindfolded, or when presenting a vestibular imbalance. However, the fact that larger heading errors were not associated with slower gait speeds in the present study suggests that speed is not an explanatory variable. It was unfortunate that gaze behavior could not be monitored in the present study. Although this limitation does not invalidate the present results, it also cannot reveal the presence or absence of an altered gaze behavior associated with the identification and control of heading direction in stroke participants.

Conclusions and Future Directions

The present results show that stroke affects the control of heading of locomotion in response to translational OFs expanding from different directions. An altered perception of heading direction and/or a poor integration of sensory and motor information are likely causes. Gaze shifts, which help in identifying heading direction through extraretinal cues, might also be involved, contributing in part to the altered heading behaviors. The altered heading responses to OF direction observed in the stroke participants may likely contribute to their steering difficulties. Future directions for research should include examining the effects of specific circumscribed brain lesions on locomotor steering behaviors as well as exploring the role of oculomotor control and the use of other sources of visual information, such as...
perceived target location, in the perception and control of locomotor heading after a brain lesion.

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**Authors’ Note**

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**Declaration of Conflicting Interests**

The authors declared no conflicts of interest with respect to the authorship and/or publication of this article.

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