Neuroscience 347 (2017) 134–147

DRIFTING WHILE STEPPING IN PLACE IN OLD ADULTS: ASSOCIATION OF SELF-MOTION PERCEPTION WITH REFERENCE FRAME RELIANCE AND GROUND OPTIC FLOW SENSITIVITY

CATHERINE P. AGATHOS, [a,b,c*] DELPHINE BERNARDIN, [c†] KONOGAN BARANTON, [c] CHRISTINE ASSAIANTE [d,e] AND BRICE ISABLEU [a,b‡]

[a] *CIAMS, Université Paris-Sud, Université Paris-Saclay, Orsay, France*

[b] *CIAMS, Université d'Orléans, Orléans, France*

[c] *Vision Sciences Department, Essilor International R&D, Paris, France*

[d] *LNC UMR 7291, Aix-Marseille Univ, CNRS, Marseille, France*

[e] *FR 3512, Aix-Marseille Univ, CNRS, Marseille, France*

Abstract—Optic flow provides visual self-motion information and is shown to modulate gait and provoke postural reactions. We have previously reported an increased reliance on the visual, as opposed to the somatosensory-based egocentric, frame of reference (FoR) for spatial orientation with age. In this study, we evaluated FoR reliance for self-motion perception with respect to the ground surface. We examined how effects of ground optic flow direction on posture may be enhanced by an intermittent podal contact with the ground, and reliance on the visual FoR and aging. Young, middle-aged and old adults stood quietly (QS) or stepped in place (SIP) for 30 s under static stimulation, approaching and receding optic flow on the ground and a control condition. We calculated center of pressure (COP) translation and optic flow sensitivity was defined as the ratio of COP translation velocity over absolute optic flow velocity: the visual self-motion quotient (VSQ). COP translation was more influenced by receding flow during QS and by approaching flow during SIP. In addition, old adults drifted forward while SIP without any imposed visual stimulation. Approaching flow limited this natural drift and receding flow enhanced it, as indicated by the VSQ. The VSQ appears to be a motor index of reliance on the visual FoR during SIP and is associated with greater reliance on the visual and reduced reliance on the egocentric FoR. Exploitation of the egocentric FoR for self-motion perception with respect to the ground surface is compromised by age and associated with greater sensitivity to optic flow.

Key words: aging, self-motion perception, optic flow, frames of reference, stepping in place, ground surface.

INTRODUCTION

Self-motion perception is important for interacting with one's environment in daily life, whether this is simply for maintaining postural balance, walking or performing more complex tasks such as intercepting a moving object. 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 et al., 1988, 2001). In ecological situations, forward or backward movements of the body elicit approaching or receding optic flow respectively, which correspond 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 perceived movements are self-initiated and not externally induced. Simulated optic flow, when walking, affects gait kinematics and heading direction (Bardy et al., 1992; Berard et al., 2009; Chou et al., 2009; Mohler et al., 2007; Pailhous et al., 1990; Prokop et al., 1997). 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 visual perception of faster self-motion (Konczak, 1994; Prokop et al., 1997; Baumberger et al., 2000; Francois et al., 2011). Similarly, an underestimation of self-motion speed arises when faced with receding flows, should the visual information be considered credible, even though such stimuli are less common and are not ecologic when moving forward. Indeed, some studies report an increase in walking speed when faced with receding flows (Konczak, 1994; Prokop et al., 1997; Baumberger et al., 2000; De Smet et al., 2009). The natural optic flow generated during quiet stance is oscillatory, which is why oscillatory stimuli are often employed when examining the contribution of dynamic cues to postural

*Correspondence to: C. P. Agathos, Vision Sciences Department, Essilor International R&D, 13 rue Moreau, 75012 Paris, France.
E-mail address: cpagathos@gmail.com (C. P. Agathos).
† Present address: Essilor/CRSNG, University of Montreal Industrial Chair,Montreal, Canada.
‡ Present address: PSYCLE, Aix Marseille Univ, Aix-en-Provence, France.

Abbreviations: ANOVA, analysis of variance; COP, center of pressure; FoR, frame of reference; QS, quiet standing; RBT, Rod and Body Test; RDT, Rod and Disk Test; RFT, Rod and Frame Test; SIP, stepping in place; VSQ, visual self-motion quotient.

http://dx.doi.org/10.1016/j.neuroscience.2017.01.044
0306-4522/

control (Bardy et al., 1996; Borger et al., 1999; Dijkstra et al., 1994; Eikema et al., 2012; Hanssens et al., 2013; Keshner and Kenyon, 2000; Lee and Lishman, 1975; Stoffregen, 1985). In these studies, participants experienced the optic flow as if it were due to their own movements and therefore swayed in the same direction as the stimulus in order to cancel the difference in perceived self-motion speed. Such directional postural responses have been observed in studies employing linear flows as well, in addition to increased postural variability with respect to natural conditions (Lestienne et al., 1977; Berthoz et al., 1979; Bronstein, 1986; Flückiger and Baumberger, 1988; Sundermier et al., 1996; Baumberger et al., 2004; Palmisano et al., 2009; Wei et al., 2010; Holten et al., 2013).

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 (Teasdale et al., 1991; Bugnariu and Fung, 2007) and walking (Konczak, 1994; Schubert et al., 2005; Chou et al., 2009). Others report a greater perturbation effect in old adults in stance (Wade et al., 1995; Sundermier et al., 1996; Borger et al., 1999; Sparto et al., 2006; O'Connor et al., 2008) and a reduced ability to exploit heading information when walking (Warren et al., 1989; Berard et al., 2009). However, studies agree that old adults are more destabilized under concurrent visual and somatosensory perturbation and have slower or reduced sensory reweighting capacities (Teasdale et al., 1991; Hay et al., 1996; Borger et al., 1999; Simoneau et al., 1999; Sparto et al., 2006; O'Connor et al., 2008; Slaboda et al., 2011).

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 fulfill perception–action relationships. Moreover, the ability to perceive and control one's spatial orientation is based on the functional alignment of body axes either on directions within a gravito-inertial field or on surrogates of the direction of gravity, such as invariant axes and planes within the visual frame of reference (Kluzik et al., 2005; Fourre et al., 2009; Isableu et al., 2009, 2010). The ground surface in particular bears special ecological relevance as it is considered an invariant source of information, i.e. a reference, for postural control via both the visual (Gibson, 1950) and podokinetic systems (Gurfinkel et al., 1995; Kluzik et al., 2007). The ecological relevance of visual information from the ground surface has been demonstrated in terms of greater processing efficiency by the visual system (Flückiger and Baumberger, 1988), as a reference for the perception of 3D layout (Bian et al., 2005) as well as offering an advantage in visual tasks, such as apparent motion perception (Osaka, 1993) and visual search (Mccarley and 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 (Gurfinkel et al., 1995; Kluzik et al., 2005, 2007), rotation (Weber et al., 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 (Guerraz et al., 1998a, 1998b; Fourre et al., 2009; Pagano and Turvey, 1995; Guerraz et al., 2000). 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 frame of reference in young adults has been linked to greater postural reactions under simultaneous visual and somatosensory perturbation, and reduced reweighting ability (Isableu et al., 2010, 2011; Slaboda et al., 2011; Brady et al., 2012; Slaboda and Keshner, 2012). Furthermore, it has been reported that reliance on the visual frame of reference increases with age (Straube et al., 1988; Sundermier et al., 1996; Agathos et al., 2015). Indeed, greater reliance on the visual reference frame has been demonstrated in old adults showing difficulties in dynamic sensory reweighting, suggesting that old adults utilize visual rather than somatosensory-based egocentric modes of spatial referencing (Slaboda et al., 2011; Eikema et al., 2012).

Studies examining old adults' postural reactions to perturbing visual information, via artificial optic flow (with or without concurrent somatosensory perturbation), have highlighted these participants' greater sensitivity to and reliance on visual cues for postural control (e.g. Borger et al., 1999; Franz et al., 2015). However, such studies have not revealed whether visual information is preferentially used as a reference to control action. By examining whether optic flow direction-specific responses are enhanced with age, we may better understand whether old adults exploit the visual FoR to a greater extent than young adults for postural control. In our study, we wanted to characterize the reported age–related increased perceptual reliance on visual information with possible associated motor signatures. Specifically, we were interested in whether and how ground optic flow perception affects motor behavior 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 optic flow generated by the body's translation, sway and bounce is a more salient self-motion signal, compared to stance. The gravito-inertial force sensed by the vestibular system is more prominent as well, but it also contains more noise, as the signal is more variable, adding hence some uncertainty in the mode of spatial referencing which aims to control body orientation and motion with respect to gravity. 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 and uncertainty is conveyed in the somatosensory signal