Optic Flow in Postural Control

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Optic flow stimuli are crucial for the control of stance in the upright position. The visual control of posture has recently received a lot of interest from several researchers. One of the most intriguing aspects is the contribution of the different parts of the visual field in the control of stance.

Keywords: quiet stance ; visual-motion processing ; self-motion perception ; body sway

1. Introduction

Different optic flow patterns provide important information about self-motion [1]. In 1950, James J. Gibson introduced the concept of "optic flow" to describe the visual stimulation provided to an observer who moves through the extra-personal space [2][3].

Within the cortical network, the optic flow input is integrated with other somato-sensory signals to guide locomotion and to maintain correct posture [4]. The somatosensory input originates from the proprioceptive signals of muscles and joints, whereas the vestibular input originates from the linear and rotational acceleration of the head relative to the body [5]. Optic flow is a complex visual array with specific spatial and temporal characteristics, like geometric structure, amplitude, speed, frequency, and location in the visual field (such as the foveal or peripheral regions). All these features can influence evoked postural responses [6][7][8][9][10][11][12][13][14][15]. The physiological mechanisms within the neural network integrate optic flow and other somato-sensory signals to generate a typical body oscillation, which has been called "body sway". Indeed, several studies have shown that visual stimulation evokes body sway [16][17][18][19][20][21]. These small postural oscillations reflect the regulatory activity of several control loops responsible for the control of posture [4][22].

It is known that in somato-sensory integration, the optic flow visual stimuli play a fundamental role in the maintenance of quiet stance in the upright position [11]. Changes in the visual input, such as passing from a dark to light environment, or directional changes such as from a forward to backward locomotion, require an updating of the sensory integration in order to provide the motor cortex with precise and consistent information about both the extra-personal space and the internal state [5][7][12][23]. Thus, a motor action consists of many interconnected contributing factors [11].

2. Optic Flow

The optic flow visual signal is created by the relative motion between an observer who moves through the environment and the environmental structures [2]. The extra-personal space consists of objects bounded by surfaces and visual perception is possible because light is reflected by such surfaces. In most cases, light is not reflected uniformly. Instead, it originates from a densely structured optical array at the point of observation. The optical array can be thought of as a bundle of narrow light cones, with their apices at the observation point [24]. Each cone has, as its basis, an element of distinct environmental texture and is therefore optically differentiable from its neighbors in terms of the intensity and the spectral composition of the light it contains. In each observation point there is a unique optical array. As a result, when the head or the eye moves relative to the environment, the optical array to the eye changes continuously over time, giving rise to an optical flow field.

Gibson showed that when an observer moves through the environment, the visual motion in the optical array expands radially from a single point, known as the "focus of expansion" (FOE), which has an important role in heading perception. The FOE is the point in the distance where the optic flow originates, thus in the FOE there is no flow. When an observer moves through the environment while fixating on his/her final destination, the visual perception of self-motion is mainly due to the FOE of the optic flow field. However, in daily life, self-motion perception requires the combination of different brain functions, given that eye and head movements change the FOE position with respect to the fovea.

The information provided by the optic flow input is necessary to encode the heading direction, spatial orientation and self-motion perception in the three-dimensional space [3][25]. Optic flow becomes absolutely important for the control of posture and locomotion, and for the selection of the appropriate motor actions [15][17][24][26]. Every transformation of the retinal input provides the observer with an experience of a movement. In the laboratory experimental condition, we usually have an immobile observer who views the optic flow stimuli projected on a screen. Thus, an expanding optic flow simulates a condition in which the observer moves forward, whereas a contracting optic flow simulates a condition in which the observer moves backward [27][28][29][30][31][32][33][34][35]. The processing of the perception of a movement is different in the retina, the brain or in the consciousness, because vision is a sensory-dependent variable of experience [2].

3. The Important Role of Optic Flow in Postural Control

In the last decade, the role of optic flow in the control of posture has received more and more interest from the scientific community and the research on many aspects has been advancing. Many factors have to be considered in the generation of the experimental paradigm, including the dimension of the stimulated visual field, the type of optic flow stimuli used (i.e., moving dots, moving stripes), and the duration of the stimulation.

This review focuses on an important aspect to take into account: the dimension of the stimulated visual field. The choice of the exact portion of the retina to be stimulated is crucial given that the stimulation of the different central and the peripheral parts of the retina leads to the activation of different geniculo-cortical pathways, which prompts different cortical processing of information, and thus results in a differential activation of motor pathways.

Until now, several studies have been aimed at uncovering the functional roles of the peripheral and central visual fields in postural control, leading to different conclusions. Many authors have already pointed out that such differences and the controversial results are likely to have arisen from the different experimental protocols and approaches.

According to the retinal distribution of cone and rod photoreceptors, the definition of central vision ranges between 2° and 4° of the visual field [36]. In the retina, the density of the cone photoreceptors decreases as the distance from the fovea increases [37][38]. However, considering that projections from the retina to the cortical area are responsible for processing central vision, the central visual field has been defined as the 7° surrounding the fovea, thus including the foveal, parafoveal and perifoveal regions [39].

Besides the different definitions of the central and peripheral visual fields, the visual stimuli and the methodologies also differed across studies. In some studies, the stimuli were formed by random dot patterns, whereas in other studies, the stimuli were formed by vertical moving bars. In the majority of the studies, the stimuli were projected on a screen placed in front of the participants, whereas in other studies, the stimuli either originated from a side of the visual field or from placing subjects in a room with moving walls. The following chapters specify the protocols and definitions adopted by each study reported in this review, trying to explain how the different protocols conditioned the results.

4. Visual Pathways

Uncovering the role of optic flow in postural control, and more specifically, elucidating the functional differences between the central and peripheral visual fields, is challenging due to the complex anatomo-physiological organization of the mammalian retina. Anatomical studies showed that each retinal area projects to different cortical pathways. It is thought that the primate retina contains more than 20 types of ganglion cells, most of which are unstudied. Dannis Dacey reported that there are three main types of ganglion cells projecting to the lateral geniculate nucleus: the parasol, the midget and the small bistratified cells [40]. As reported by Dacey in 1994, the relative densities of the three types of ganglion cells vary in eccentricity. In the fovea, the midget cells represent about 90% of the total ganglion cells, the parasol cells about 5% and small bistratified cells about 1%. On the contrary, the peripheral retina is formed for the major part by the midget cells, which are the 45–50% of the total ganglion cells, the parasol cells are about 20% and the small bistratified cells are about 10%. Thus, from the peripheral to the central retina, the number of midget ganglion cells progressively increases relative to the parasol and the small bistratified types [40]. The parasol cells project to the geniculate magnocellular layers while the midget and the bistratified cells project to the geniculate parvocellular layers.

In the lateral geniculate nucleus, the parvocellular and magnocellular layers originate from two different pathways, namely the ventral and dorsal visual streams, respectively. The ventral stream, which mostly originates from the fovea, processes information related to the color and shape of objects; it is also called the “what” pathway. On the other hand, the dorsal stream, which mostly originates from the peripheral regions of the retina, processes information related to self-motion perception, depth, and spatial orientation; it is also called the “where” pathway [41][42][43][44].

Dearing and Harris already reported that the view that the peripheral visual field is crucial in generating vection has been challenged [45]. A reasonable behavioral explanation for the periphery being more important in perceptual orientation arises from the observation that the peripheral visual field is not usually occluded by objects of interest. In addition, salient features that are relevant for motion perception, like walls or floors, are more visible in this region.

It thus becomes clear that a precise anatomical distinction between the foveal (or central) and peripheral retinal fields is necessary for developing an appropriate experimental protocol to study the contribution of optic flow in postural control. Even the inclusion of a few degrees of visual angle in either the peripheral or central visual fields could change the results and lead to contradictory findings.

References

1. Lappe, M.; Bremmer, F.; van den Berg, A.V. Perception of self-motion from visual flow. Trends Cogn. Sci. 1999, 3, 329–336.
2. Gibson, J.J. The Perception of the Visual World; Houghton Mifflin: Boston, MA, USA, 1950.
3. Gibson, J.J. The visual perception of objective motion and subjective movement. Psychol. Rev. 1954, 61, 304–314.
4. Peterka, R.J.; Benolken, M.S. Role of somatosensory and vestibular cues in attenuating visually induced human postural sway. Exp. Brain Res. 1995, 105, 101–110.
5. Yamada, M.; Higuchi, T.; Mori, S.; Uemura, K.; Nagai, K.; Aoyama, T.; Ichihashi, N. Maladaptive turning and gaze behavior induces impaired stepping on multiple footfall targets during gait in older individuals who are at high risk of falling. Arch. Gerontol. Geriatr. 2012, 54, e102–e108.
6. Brandt, T.; Dichgans, J.; Koenig, E. Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. Exp. Brain Res. 1973, 16, 476–491.
7. Dijkstra, T.M.; Schöner, G.; Gielen, C.C. Temporal stability of the action-perception cycle for postural control in a moving visual environment. Exp. Brain Res. 1994, 97, 477–486.
8. Dijkstra, T.M.; Schöner, G.; Giese, M.A.; Gielen, C.C.A.M. Frequency dependence of the action-perception cycle for postural control in a moving visual environment: Relative phase dynamics. Biol. Cybern. 1994, 71, 489–501.
9. Kiemel, T.; Oie, K.S.; Jeka, J.J. Multisensory fusion and the stochastic structure of postural sway. Biol. Cybern. 2002, 87, 262–277.
10. Lestienne, F.; Soechting, J.; Berthoz, A. Postural readjustments induced by linear motion of visual scenes. Exp. Brain Res. 1977, 28, 363–384.
11. Peterka, R.J. Sensorimotor integration in human postural control. J. Neurophysiol. 2002, 88, 1097–1118.
12. Stoffregen, T.A. Flow structure versus retinal location in the optical control of stance. J. Exp. Psychol. Hum. Percept. Perform. 1985, 11, 554–565.
13. Stoffregen, T.A. The role of optical velocity in the control of stance. Percept. Psychophys. 1986, 39, 355–360.
14. Stoffregen, T.A.; Schmuckler, M.A.; Gibson, E.J. Use of central and peripheral optic flow in stance and locomotion in young walkers. Perception 1987, 16, 113–119.
15. Van Asten, W.N.; Gielen, C.C.; van der Gon, J.J.D. Postural adjustments induced by simulated motion of differently structured environments. Exp. Brain Res. 1988, 73, 371–383.
16. Bronstein, A.M. Suppression of visually evoked postural responses. Exp. Brain Res. 1986, 63, 655–658.
17. Lee, D.; Lishman, J.R. Visual proprioceptive control of stance. J. Hum. Mov. Stud. 1975, 1, 87–95.
18. Persiani, M.; Piras, A.; Squatrito, S.; Raffi, M. Laterality of stance during optic flow stimulation in male and female young adults. BioMed Res. Int. 2015, 2015, 542645.
19. Piras, A.; Raffi, M.; Perazzolo, M.; Squatrito, S. Influence of heading perception in the control of posture. J. Electromyogr. Kinesiol. 2018, 39, 89–94.
20. Raffi, M.; Piras, A.; Persiani, M.; Perazzolo, M.; Squatrito, S. Angle of gaze and optic flow direction modulate body sway. J. Electromyogr. Kinesiol. 2017, 35, 61–68.
21. Raffi, M.; Piras, A.; Persiani, M.; Squatrito, S. Importance of optic flow for postural stability of male and female young adults. Eur. J. Appl. Physiol. 2014, 114, 71–83.
22. Collins, J.J.; de Luca, C.J. The effects of visual input on open-loop and closed-loop postural control mechanisms. Exp. Brain Res. 1995, 103, 151–163.

23. Martin, O.; Gascuel, J.D. Reactive Ocular and Balance Control in Immersive Visual Flows: 2D vs. 3D Virtual Stimuli. Stud. Health Technol. Inform. 2009, 144, 208–210.

24. Lee, D.N. The optic flow field: The foundation of vision. Phil. Trans. R. Soc. Lond. B 1980, 290, 169–179.

25. Gibson, J.J. Visually controlled locomotion and visual orientation in animals. Br. J. Psychol. 1958, 49, 182–194.

26. Lee, D.N.; Craig, C.M.; Grealy, M.A. Sensory and intrinsic coordination of movement. Proc. R. Soc. B Biol. Sci. 1999, 266, 2029–2035.

27. Duffy, C.J.; Wurtz, R.H. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large field stimuli. J. Neurophysiol. 1991, 65, 1329–1345.

28. Duffy, C.J.; Wurtz, R.H. Sensitivity of MST neurons to optic flow stimuli. II. Mechanism of response selectivity revealed by small-field stimuli. J. Neurophysiol. 1991, 65, 1346–1359.

29. Raffi, M.; Carrozzini, C.; Maioli, M.G.; Squatrito, S. Multimodal representation of optic flow in area PEc of macaque monkey. Neuroscience 2010, 171, 1241–1255.

30. Raffi, M.; Maioli, M.G.; Squatrito, S. Optic flow direction coding in area PEc of the behaving monkey. Neuroscience 2011, 194, 136–149.

31. Raffi, M.; Persiani, M.; Piras, A.; Squatrito, S. Optic flow neurons in area PEc integrate eye and head position signals. Neurosci. Lett. 2014, 568, 23–28.

32. Raffi, M.; Piras, A.; Calzavara, R.; Squatrito, S. Area PEc Neurons Use a Multiphasic Pattern of Activity to Signal the Spatial Properties of Optic Flow. BioMed Res. Int. 2017, 2017, 6495872.

33. Raffi, M.; Siegel, R.M. A functional architecture of optic flow in the inferior parietal lobule of the behaving monkey. PLoS ONE 2007, 2, e200.

34. Raffi, M.; Squatrito, S.; Maioli, M.G. Neuronal responses to optic flow in the monkey parietal area PEc. Cereb. Cortex 2002, 12, 639–646.

35. Siegel, R.M.; Read, H.L. Analysis of optic flow in the monkey parietal area 7a. Cereb. Cortex 1997, 7, 327–346.

36. Osaka, N. Peripheral Vision. In New Sensation Perception Psychology Handbook; Oyama, T., Imai, S., Wake, T., Eds.; Seishin-Shobou: Tokyo, Japan, 1994; pp. 923–930.

37. Curcio, C.A.; Sloan, K.R.; Kalina, R.E.; Hendrickson, A.E. Human photoreceptor topography. J. Comp. Neurol. 1990, 292, 497–523.

38. Curcio, C.A.; Sloan, K.R.; Packer, O.; Hendrickson, A.E.; Kalina, R.E. Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. Science 1987, 236, 579–582.

39. Mishkin, M.; Ungerleider, L.G. Contribution of striate inputs to the visuospatial functions of parietopreoccipital cortex in monkeys. Behav. Brain Res. 1982, 6, 57–77.

40. Dacey, D.M. Physiology, morphology and spatial densities of identified ganglion cell types in primate retina. Ciba Found. Symp. 1994, 184, 12–28.

41. Gattass, R.; Rosa, M.G.; Sousa, A.P.; Pinon, M.C.; Fiorani, M.J.; Neuenschwander, S. Cortical streams of visual information processing in primates. Braz. J. Med. Biol. Res. 1990, 23, 375–393.

42. Goodale, M.A.; Milner, A.D. Separate visual pathways for perception and action. Trends Neurosci. 1992, 15, 20–25.

43. Ungerleider, L.G.; Haxby, J.V. 'What' and 'where' in the human brain. Curr. Opin. Neurobiol. 1994, 4, 157–165.

44. Ungerleider, L.G.; Mishkin, M. Two cortical visual systems. In Analysis of Visual Behaviour; Ingle, D.J., Goodale, M.A., Mansfield, R.J.W., Eds.; MIT Press: Cambridge, MA, USA, 1982.

45. Dearing, R.R.; Harris, L.R. The contribution of different parts of the visual field to the perception of upright. Vis. Res. 2011, 51, 2207–2215.